THE STATUS AND ECOLOGY OF THE ANGONOKA TORTOISE
(*GEOCHELONE YNIPHORA*) OF WESTERN MADAGASCAR

By

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An investigation of the status and ecology of the rare angonoka tortoise

(*Geochelone yniphora*) was conducted in western Madagascar from October 1993

through June 1995. Ten tortoise localities were identified based on regional field

surveys, and 145 tortoises were observed. The 10 localities represent at least five

separate populations, all located within a 30-km radius of Baly Bay (lat. 16° 2'S, long.

45° 20'E). Juvenile tortoises were observed in all populations indicating that

reproduction is occurring throughout the range. The five populations occur on patches of

bamboo-scrub habitat that range in size from <50 ha to 4,000-6,000 ha. The habitat

patches are isolated from one another by extensive savanna and Baly Bay. No collection

of tortoises was observed in this study and exploitation probably is not a problem at this

time. However, the bamboo-scrub habitat at all areas visited appeared to have been degraded by frequent brush fires.

Ninety-nine angonoka (14 adult males, 27 adult females, and 58 juveniles) were marked on Cape Sada where monthly surveys were conducted. The population density (0.66 tortoises per ha) was low compared to other tortoise species. Nearly 40 % of tortoises on Cape Sada were juveniles < 85 mm carapace length. A lack of intermediate sized tortoises and the observation of dead juveniles suggests that juvenile mortality in this population is high.

Tortoises were most active (e.g., walking, mating, nesting, and feeding) in the wet season (November – April) when food and water were abundant, whereas in dry season (May – October) tortoises usually were resting under vegetative cover. Patches of grass offered important cover sites for angonoka in the dry season, whereas open rocky areas were important feeding sites during the wet season.

The angonoka is threatened with extinction in the wild, primarily because of its small population size and extremely limited geographic distribution. A catastrophic event such as disease or severe weather could cause extinction of some or all populations. Removal of adult tortoises from remaining populations also could have a severe impact on the survival of this species. Long-term survivorship data are needed to determine whether populations are increasing. However, recovery of the species will be limited by the amount of available habitat. Therefore, conservation efforts should focus not only on physically protecting angonoka, but also on protecting and restoring the bamboo-scrub habitat.

CHAPTER 1
INTRODUCTION

<u>Madagascar- An Island Continent</u>

The island of Madagascar has been called a microcontinent because of its large size, long history of isolation, and diverse environment (Paulian 1984). It is the fourth largest island in the world, encompassing an area nearly 600,000 km^2 in size (Battistini 1972). The island rifted from Africa, near present day Somalia, in the mid-to-late Jurassic (ca. 165 million years ago). It achieved its current position, more than 400 km east of Mozambique, in the early Cretaceous (ca. 121 mya) (Rabinowitz et al. 1983; Coffin and Rabinowitz 1987; Reeves et al. 1987; Krause et al. 1997). Madagascar and the Indian subcontinent separated in the late Cretaceous, ca. 88 mya (Storey et al. 1995). Most of the extant fauna has clear affinities with Africa, and the founding stock of these species are thought to have rafted across the Mozambique Channel after the island attained its current position (Jolly et al. 1984). Other species (e.g., the mollusks, some birds, frogs, and bats) have Indo-Malayan affinities (Benson 1984; Paulian 1984; Langrand 1990) and a few species (e.g., iguanids and boids) are most closely allied with groups in South America (Paulian 1984). More than 90 % of Madagascar's forest species are unique to the island (Jolly et al. 1984). Of the more than 300 species of reptiles in Madagascar, 95 % are endemic to the island or to the region (Blanc 1972; Blanc 1984; Raxworthy and Nussbaum

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1997). In addition to a high degree of endemism, Madagascar contains a major portion of the world's biological diversity (Myers 1986; Mittermeier 1988).

Humans arrived on Madagascar approximately 1,500-2,500 years ago (Battistini and Vérin 1972; MacPhee and Burney 1991). The Malagasy people share an African and Indonesian origin, and at least 20 regional ethnic groups occur on the island (Rakotoarisoa 1986). Today more than 14 million people inhabit Madagascar and the population growth rate is somewhere between 2-3 % annually (Bos et al. 1994; United Nations 1997). Since the island was settled, at least 23 species of animal have become extinct, including the island's megafauna. Two giant tortoises (*Dipsochelys abrupta* and *D. grandidieri*), flightless elephantbirds (*Aepyornis* spp.), and giant lemurs (*Megaladapsis* spp.) all have been lost (Mahé 1972; Burney and MacPhee 1988; Burney 1993; Bour 1994). The issue of whether or not the recent extinctions were caused by human or climatic changes has been debated heavily (Burney 1993; Dewar 1997; MacPhee and Marx 1997). In addition to the recent extinctions, much of the island's original forest has been replaced with manmade grasslands. Early estimates were that humans had cleared as much 80 % of Madagascar's forest cover (Jolly 1980; Jenkins 1987). However, grasslands in western Madagascar may actually pre-date the arrival of humans on the island (MacPhee et al. 1985; Burney and MacPhee 1988; Burney 1997). Nonetheless, today the forests and other natural communities of Madagascar are declining and much of the remaining wildlife is critically endangered (Jenkins 1987).

Geochelone yniphora- The Angonoka Tortoise

The reptile fauna of Madagascar includes four endemic tortoises, *Geochelone radiata*, *G. yniphora*, *Pyxis arachnoides*, and *P. planicauda*. Humans introduced a fifth species, *Kinxys belliana*, to the island from mainland Africa 1,000-1,500 years ago (Kuchling 1986; Glaw and Vences 1994). None of the endemic species are well known, and all four species probably are threatened. *Geochelone radiata*, the radiated tortoise, and *P. arachnoides*, the spider tortoise, are the most widely distributed of the four species. These two species occur in the dry thorn scrub of southern Madagascar. Radiated tortoises still occur in reasonably high densities in a few areas but are harvested for food, exported illegally for the pet trade (Durrell et al. 1989a; J. Behler, pers. com.), and killed on roads (Goodman et al. 1994). Spider tortoises typically are not exploited for food because of traditional taboos against eating them (Juvik 1975*)*; however, local taboos are apparently breaking down and this species may become increasingly exploited in the future (J. Behler, pers. com.). *Pyxis planicauda*, the flat-tailed tortoise, occurs only in dry deciduous lowland forests near Morondava in west central Madagascar (Behler et al. 1993). Deciduous dry forests are extremely fragmented and degraded and only about 15,000 ha of suitable flat-tailed tortoise habitat remains (Kuchling and Bloxam 1988).

Geochelone yniphora, the "angonoka" or ploughshare tortoise, is the largest of Madagascar's extant tortoises. This species received its English common name for the distinctive long, plow-like gular projection of adult males. The angonoka is arguably one

of the rarest tortoises in the world (Angel 1931; Juvik et al. 1981; Groombridge 1982; Curl 1986a; Durrell et al. 1989b). It was declared a protected species by the Malagasy government in 1931, and is listed as Endangered in the IUCN Red List of Threatened Animals (IUCN 1996). All historic localities of *G. yniphora* occur within a very restricted area in the vicinity of Baly Bay in western Madagascar (Figure 1-1) (Blanc 1974; Juvik et al. 1981; Curl et al. 1985).

 Geochelone yniphora and *G. radiata* were placed in the subgenus *Asterochelys* based on similarities in osteology and shell morphology (Loveridge and Williams 1957). Crumly (1982) later described a possible sister relationship between *G. yniphora* and *Geochelone pardalis*, an African species. He also found similarities between *Dipsochelys dussumieri* (a species from Aldabra and the Seychelles formerly referred to as *Geochelone gigantea* or *D. elephantina*) and *G. radiata*. This classification was based only on cranial osteology and is not widely accepted. A recent examination of mitochondrial DNA of the endemic Malagasy tortoises revealed that the four species may share a monophyletic origin (Caccone 1999). This suggests that there was a single colonization event by an ancestral Testudinid. This ancestral tortoise probably rafted from Africa approximately 22-14 mya. The *Pyxis* clade is thought to have diverged from the ancestral form ca. 12-8 mya and the *G. yniphora* and *G. radiata* clade diverged in the Pliocene (ca. 5 mya). Juvik et al. (1981) speculated that the divergence of *G. yniphora* and *G. radiata* occurred during the Pleistocene (ca. 1.8 mya), and that the ancestral tortoise persisted in southern and western refugia during mesic conditions.

The present distribution of the angonoka was not discovered until the early 20th Century. This species was first described from specimens obtained from Arab sailors in the Comoro Islands in 1884 (Vaillant 1889). The specimens were thought to have originated from an island north-northeast of Comoro, in the vicinity of Aldabra. A later specimen was thought to have come from Tulear in southwest Madagascar (Vaillant 1889). The actual distribution of the species was discovered when Siebenrock (1903) described a wild specimen collected by Voeltzkow at Cape Sada in northwestern Madagascar.

Little was known of the status of wild populations of *G. yniphora* until the 1970s when a series of field surveys in the Baly Bay region were conducted (Juvik and Blanc 1974; Juvik et al. 1981). Very few angonoka were discovered in the early surveys, suggesting that the species was critically endangered. The reasons for the apparent rarity of the angonoka are not fully understood. However, past commercial exploitation may have been a contributing factor. Remains of *G. yniphora* have been recovered from archaeological sites on Maore, the easternmost island in the Comoro archipelago, indicating that this species was exploited for food as early as 900 AD (Allibert 1989). Historic records also indicate that during the 17th Century, large numbers of *G. yniphora* were exported to the Comoro Islands where they were sold as food to traveling ships (Vaillant and Grandidier 1910). Today, local people generally do not eat angonoka; however, tortoises are sometimes kept as pets (Curl et al. 1984; Durbin et al. 1996).

Anthropogenic brush fires also may have contributed to the endangered status of

the angonoka (Juvik et al. 1981; Groombridge 1982; Curl et al. 1985; Durrell et al. 1989b). Frequent, high intensity fires occasionally kill angonoka and are thought to convert the bamboo-scrub habitat of the angonoka to savanna (Curl 1986a). Brush fires are set to promote growth of grasses for free ranging cattle, to drive cattle from the forest and to maintain clearings around vegetable gardens (Durbin et al. 1996). The clearings around gardens are created to keep the non-native African bush pig (*Potamochoerus larvatus*) from destroying crops. Bush pigs are widespread in western Madagascar (Grubb 1993) and are thought to prey on eggs and young of the angonoka (Juvik et al. 1997).

Project Angonoka

In 1986, Jersey Wildlife Preservation Trust (JWPT) and the Malagasy Direction des Eaux et Forêts initiated a multifaceted conservation program for the angonoka, entitled "Project Angonoka". One of the first objectives of Project Angonoka was to establish a captive-breeding program for the angonoka in Madagascar, with the intent of augmenting wild populations with captive born offspring (Curl 1986b). The breeding program was begun with a founder stock of 20 adult tortoises that were collected from the National Zoo at Antananarivo and from villagers in the Baly Bay region who had kept tortoises as pets. As of 1998, a total of 180 offspring had been produced at the breeding center (D. Reid, pers. com.). In 1991, JWPT and the World Wide Fund for Nature (WWF) implemented a social research project to promote the protection and sustainable

use of resources in the region (Durbin and Ralambo 1994, Durbin et al. 1996). In addition, from 1989 and 1993 JWPT field teams conducted a series of field surveys to assess the status of wild angonoka populations (Reid 1989, 1990a, 1990b, 1991a, 1991b, 1993). Survey results supported the previous impression that angonoka were exceptionally rare.

The limited knowledge of the status and ecology of the angonoka made development and implementation of a conservation plan for this species difficult. Therefore, this study of wild angonoka was initiated in 1993. My primary objective was to visit historic tortoise localities and attempt to identify new localities. Results of these surveys were used to assess the overall status of the species. The second objective was to describe aspects of the life history and ecology of the angonoka. In October 1993, a field research station was established at Cape Sada. The research station was located at the east edge of the Cape Sada peninsula, less than 0.5 km from tortoise habitat. The station was used as a base camp from which regional tortoise surveys were conducted in 1994 and 1995. From 1993 through 1995, aspects of the demography, movements, and activity patterns of tortoises in the Cape Sada population were studied.

Description of Study Area

The study area, hereafter referred to as the Baly Bay region, is located on the west coast of Madagascar approximately 90-km south of the city of Mahajanga (lat. $16^\circ 2'$ S, long. $45^\circ 20'$ E). The geology of the region is characterized by recent (Eocene) alluvial

rock (Brenon 1972). Coastal areas consist of Miocene marine sediments overlain with a ferruginous lateritic crust. The average elevation in the region ranges from 10-30 m with maximum elevations from 50-80 m above mean sea level.

The climate in the Baly Bay region is tropical, with distinct wet and dry seasons. Nearly all precipitation occurs in the summer or wet season (November through April) (Donque 1972). Little or no rainfall occurs in the winter or dry season (May through November). Total annual rainfall typically is more than 1,000 mm and the highest monthly total (ca. 400 mm) usually occurs in January (Donque 1972). The mean annual temperature at the town of Soalala on Baly Bay is 26.6° C, with monthly means ranging from 26° C in July to 28° C in April. Tropical cyclones, originating in both the Indian Ocean and Mozambique Channel, frequently cross Madagascar in summer months (November-March). In western Madagascar these storms most often occur in January and February.

The original vegetation in the Baly Bay region was Western Domain dry deciduous forest (Koechlin 1972). The coastal area contains extensive mangroves (*Rhizophora* spp.). Today, the dry deciduous forest in the region is heavily fragmented and fire-maintained savanna is a major component of the area. Angonoka inhabit bamboo-scrub vegetation, a secondary stage of the dry deciduous forest (Curl et al. 1985). Bamboo-scrub habitat consists of a mosaic of shrubs, bamboo, savanna grasses, and open, unvegetated areas. The shrubs are generally less than 2-m in height, and the most common species are *Bauhinia* sp. and *Terminalia* spp. Bamboo (*Perrierbambos*

madagascariensis) occurs in dense thickets within the habitat. A few shrubs and satrana palms (*Bismarkia nobilis*) are interspersed in the bamboo thickets, but ground cover vegetation is largely absent. Small savanna-like patches and unvegetated rocky areas occur within the scrub-shrub habitat. Grasses in the savanna-like patches include *Aristida* sp., *Eragrostis* sp., and *Heteropogon contortus*.

The largest town in the region is Soalala, located on the southeastern side of Baly Bay (Figure 1-1). Soalala has about 1,000 inhabitants, most of whom are Muslim. People in surrounding coastal villages belong to the Sakalava ethnic group and are primarily small scale fishermen. Agriculture in the coastal region is limited to subsistence gardening. Historically, the Sakalava people raised large numbers of cattle (Vérin 1986). Fewer cattle are kept today than in the past; however, they are still important culturally. Cattle are used to trample fields to break up soil prior to planting rice, for religious rituals, and are traded for brides (Durbin 1993). Cattle typically range free in the savannas surrounding villages but may be hidden from cattle thieves in forest patches (Durbin 1993).

Cape Sada, where the research station was established, is a 150-ha peninsula located on the east side of Baly Bay. The maximum elevation is 50 m above mean sea level. There are no human settlements on the Cape itself, but the beaches and coastline are used seasonally by local fishermen. Cape Sada is covered in bamboo-scrub habitat, except for the northern part, which contains a dense komanga (*Erythrophleum couminga*) forest. The region east of the Cape contains extensive savanna and salt flats. Additional

information on the physiography, climate, and vegetation of the study area is presented in Chapters 2 and 3.
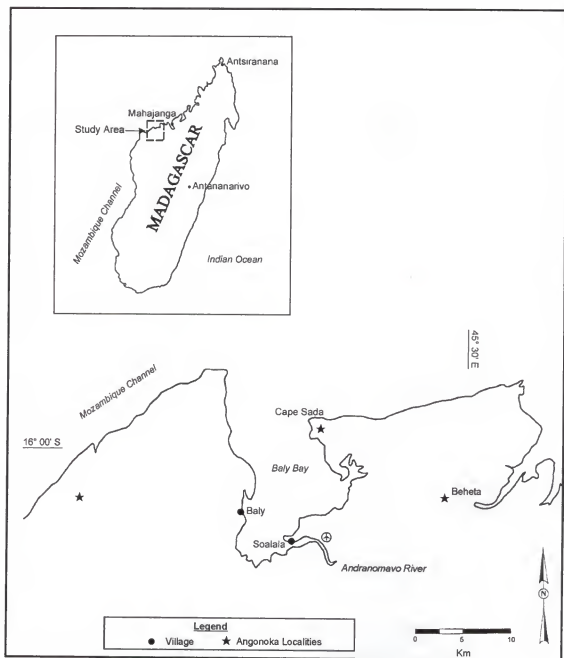
Figure 1-1. Historic localities of the angonoka tortoise (*Geochelone yniphora*) in the Baly Bay region of western Madagascar.

CHAPTER 2
STATUS AND DISTRIBUTION

Introduction

The earliest records of wild angonoka suggested that the species was exceedingly rare (Angel 1931; Siebenrock 1903). However, the first attempts to assess the status of wild angonoka populations did not take place until the 1970s. Juvik et al. (1981) visited the Baly Bay region intermittently over a 5-year period and were only able to locate five tortoises. Four tortoises were found at Cape Sada and one at Ankoro, west of Baly Bay. They also found fresh tortoise droppings at Beheta and Ambatojoby. Based on the amount of search time invested (375 person-hours), Juvik et al. (1981) estimated that the density of *G. yniphora* in the wild was probably less than five tortoises per km^2. They further estimated that less than 100-km^2 of habitat remained, and that the total population size was likely no more than a few hundred tortoises. In 1983, Curl et al. (1985) conducted 6 weeks of field surveys in the region. Tortoise localities described by Juvik et al. (1981) were re-visited, and verbal interviews with local people were conducted in an attempt to confirm the location of tortoise populations. Although they were not specific as to the number of tortoises observed in their surveys, they cautiously estimated that as few as 100-400 angonoka existed in the wild and that only 40 to 80-km^2 of bamboo-scrub habitat remained (Curl et al. 1985).

Later surveys were focused at Cape Sada, the most accessible tortoise population; however, surveys also were conducted at Beheta and at localities west of Baly Bay (Reid 1991a, 1993; Juvik et al. 1997; Hawkins and de Valois, 1993). Results of these surveys indicated that the Cape Sada population probably contained less than 30 individuals. A single tortoise was found at Beheta and another at Antsahavaky in the vicinity of Ankoro. Several tortoises at Cape Sada were radio-instrumented to monitor tortoise movements.

These historic surveys yielded basic information about the distribution of remaining angonoka populations as well as preliminary information on seasonal tortoise movements. In order to supplement the information from these early studies, this 2-year field project was initiated in 1993.

A field research station was established at Cape Sada on the eastern side of Baly Bay in October 1993. A continuous study of the ecology of the Cape Sada angonoka population was conducted from October 1993 through June 1995. The Cape Sada research station also was used as a base camp from which regional tortoise surveys were conducted in 1994. This chapter summarizes the results of the regional surveys and includes demographic data collected from the Cape Sada population. The specific goals of this portion of the study were as follows:

1. To visit all historic and potential angonoka localities in the Baly Bay region and to assess the status of the populations and the bamboo-scrub habitat.

2. To map all confirmed angonoka localities and the extent of the habitat.

3. To describe aspects of the demography of the Cape Sada angonoka population.

Methods

Field surveys were conducted from October 1994 through April 1995 at 10 localities in the Baly Bay region. Areas surveyed were chosen based on both historic records and on interviews with local villagers. Surveys were concentrated in the wet season (from November through April), when angonoka are most active (Juvik et al. 1981; Juvik et al. 1997). The localities surveyed and field trip dates are listed in Table 2-1. Monthly surveys were conducted at Cape Sada (from October 1993 to March 1995) in an attempt to mark all individuals in the population. All surveys generally were conducted between 0600-1100 hrs and 1500-1800 hrs.

The bamboo-scrub habitat of the angonoka contains impenetrable patches of shrubs and bamboo that precluded the use of formal transect surveys. Rather than clear transects through the habitat, surveys in this study consisted of timed searches for tortoises. During these searches, participants walked roughly parallel transects looking for tortoises, tracks, or feces. Transects were approximately 10-20 m apart, depending upon the density of the vegetation. In heavily vegetated areas, where visibility was low, transects were as close as necessary to search each area thoroughly. The number of survey participants ranged from three to seven individuals including trained field

assistants and guides. The observation rate for each area was calculated as the number of tortoises observed per survey-hour.

When a tortoise was encountered, the date and time of capture were recorded. Daily rainfall totals and minimum and maximum temperatures were recorded at Cape Sada. Tortoise localities were determined with an Ensign XL Global Positioning System (Trimble Navigation, Sunnyvale, CA), which was accurate to within 10-100 m. The extent of tortoise habitat in different regions was estimated using 1990 Landsat Thematic mapper digital data (Juvik et al. 1997).

Adult and subadult tortoises were marked by notching a series of marginal scutes (Cagle 1939). Hatchling and small juvenile tortoises were marked with enamel paint on the marginal scutes. Trovan Passive Integrated Transponders (RS Biotech) were implanted subcutaneously above the forelimb of tortoises greater than 100 mm carapace length. Straight-line carapace length (CL), shell height, and plastron length of tortoises greater than 100 mm were measured to the nearest 1.0 mm using Haglof Mantax aluminum calipers (Forestry Suppliers, Inc., Jackson, MS). A metric dial caliper (accurate to the nearest 0.01 mm) was used to measure CL of hatchlings and juveniles less than 100 mm in length. Scute growth rings were counted using the first or second costal plate of all tortoises, following methods outlined in Zug (1991). Growth rings were difficult to distinguish in very large tortoises; therefore, a minimum number of rings was recorded in these individuals.

The sex of adult tortoises was determined based on differences in shell morphology. Adult male angonoka have an elongated gular and a concave plastron. Also, the width of the anal fork of adult males is nearly twice that of the anal notch. These characteristics generally could be distinguished in individuals greater than 300 mm CL or with approximately 13 to 16 scute growth rings (see Chapter 5).

Results

Tortoise presence was confirmed at 10 out of 11 areas surveyed (Figure 2-1), and 145 tortoises were marked (Table 2-1). For comparative purposes, observation rates for the areas surveyed are presented in Table 2-2. Three populations east of Baly Bay were confirmed (Cape Sada, Ankasakabe, and Beheta), and at least two populations west of the Bay were identified (Betainalika and the region including Ambatomainty, Anjaha, Andrafiafaly, Antsahamena-South, Andranolava, and Antsahavaky). The distance between the closest east and west population is approximately 24-km over land, and extensive savanna and the Andranomavo River separate the two areas. Although most of the tortoises (68 %) were found on Cape Sada, where monthly surveys were conducted, the most extensive tract of contiguous angonoka habitat occurs west of Baly Bay in the region including Ambatomainty, Anjaha, Andrafiafaly, Antsahamena-South, Andranolava, and Antsahavaky. This area extends more or less unbroken from

Antsahamena in the north and Ambarindranahary in the east to Andranolava in the south.
Survey results for the 11 localities are presented below.

East Baly Bay

Cape Sada. Ninety-six tortoises were encountered on Cape Sada between 1993
and 1995. This total includes 21 of 24 tortoises that were marked by JWPT field teams
prior to 1993 (three tortoises that had been marked in previous surveys were not
recaptured in this study). A total of 1,297.25 survey hours were conducted over the
period. Of the 99 individuals marked on Cape Sada, 14 were adult male, 27 were adult
female and 58 were juveniles less than 300 mm CL. The sex ratio among adult tortoises
was 1:1.93 and differed significantly from 1:1 (χ^2= 4.05, df= 1, P= 0.04).

The mean CL of adult male tortoises on Cape Sada was 409.6 mm (n=14, range =
282.0-456.0, SD = 45.0) as compared to 361.8 mm in adult females (n= 26, range =
285.0- 405.0, SD = 29.0) (Table 2-3). Tortoises classified as juveniles ranged in size
from 43.5 mm CL to 310.0 mm CL. Sixteen of the 58 juveniles were hatchlings that
were measured as they emerged from nests. The mean CL of newly emerged hatchlings
was 47.2 mm (n=16, range = 43.5 – 52.0, SD = 3.0).

Nearly 40 % of the tortoises captured on Cape Sada were juveniles with less than
85 mm CL (Figure 2-2), indicating that successful reproduction is occurring in this
population. However, only 22 % of the tortoises were in intermediate size classes (84.8-

322 mm CL). Although it is possible that intermediate sized tortoises were simply more difficult to find than adults or small juveniles, I suspect that these tortoises were underrepresented in surveys because survivorship of hatchlings and juveniles is very low. The partial remains of 22 dead juvenile angonoka were found during monthly surveys on Cape Sada. The remains of 15 of the 22 dead juvenile tortoises consisted of only a few scutes and the cause of mortality could not be determined. However, five of the dead juveniles with 2-3 scute growth rings appeared to have been killed by birds of prey or small mammals. Potential predators of small juvenile angonoka include the Madagascar buzzard *(Buteo brachypterus)*, common tenrec (*Tenrec ecaudatus*), fosa (*Cryptoprocta ferox*), and introduced species such as civet cat (*Viverricula indica*), and black rat (*Rattus rattus*). Local people claim that boa (*Boa "Acrantophis" madagascariensis*) and yellow-billed kite (*Milvus migrans*) also are predators of young angonoka (Juvik et al. 1981). Two juveniles with 5 and 7 scute growth rings (approximately 70-100 mm CL) may have been killed by a large predator. The shells of these tortoises had been broken between bone sutures and large puncture wounds were present. The fosa is the largest native carnivore in Madagascar (Garbutt 1999); however, adults of this species weigh less than 10 kg, and it is unlikely that they could kill and consume large juvenile angonoka. African bush pigs have a head length of approximately 350 mm and probably are capable of killing large juvenile angonoka (Oliver 1993). However, the tortoises may have died of other causes and simply been scavenged by African bush pigs.

Tracks, feces, and digging of African bush pigs often were observed on Cape Sada, particularly during the wet season. Twelve angonoka nests were monitored for disturbance by predators during this study (see Chapter 4); however, no direct evidence of egg predation was observed. In a subsequent study at Cape Sada, a nest containing three eggs was destroyed by bush pigs (Pedrono 1996).

During monthly surveys, tortoises were most frequently observed in January, when, on average, a tortoise was encountered every 4 survey-hours. High observation rates generally corresponded with months of high rainfall (Figure 2-3). A comparatively high observation rate among adult tortoises in October probably reflected breeding activity (see Chapter 4). A large proportion of adult female tortoises was observed in May during peak nesting season. Many juvenile angonoka (with 1-3 shell growth rings) were observed in open areas in February and March. Very few tortoises were encountered during June, July, and August, the height of the dry season. The radio-telemetry study revealed that tortoises were inactive during these months, typically resting beneath vegetation (see Chapter 3).

Although fire scars were evident on some of the large trees on Cape Sada, the area probably had not burned since the earliest JWPT field surveys in 1988 (Reid 1989). However, a brush fire on Cape Sada after our study resulted in the death of at least one adult tortoise (L. Durrell, pers. com.).

Juvik et al. (1997) described three populations of angonoka at Cape Sada that inhabited "open scrub forest habitat" in the north, central and southern portion of the peninsula. However, during monthly surveys I found that tortoises often moved between the open scrub areas delineated by Juvik et al. (1997) and also used the dense bamboo thickets dividing them. Therefore, I feel that Cape Sada hosts a single population of angonoka. The number of unmarked tortoises observed on Cape Sada declined steadily from February through March 1995 (Figure 2-4) and no unmarked tortoises were found during the last three months of the study. It is likely that nearly all adult tortoises in the population have been marked, but some juvenile tortoises may have been missed. The Cape Sada peninsula is roughly 150-ha in size and the estimated tortoise density is 0.66 tortoises per ha.

A small patch of bamboo-scrub habitat occurs east of the Cape Sada peninsula. Juvik et al. (1997) reported finding old tortoise droppings in this area during a 1992 survey. However, nearly 80 survey-hours were spent in this area during the 1993-94 wet season and no tortoises or tortoise sign was observed.

Ankasakabe. Two adult male tortoises were observed at Ankasakabe in 32.5 survey hours in April 1995, yielding an observation rate of 0.06 tortoises per survey-hour (Table 2-2). This value is slightly less than that of Cape Sada during April surveys. Tracks of juvenile tortoises were seen on two occasions at Ankasakabe. The presence of juvenile tortoises indicates that a breeding population still exists at Ankasakabe.

However, I suspect that the population is very small because the tortoise habitat is less than 50 ha in size and contains only a few stands of bamboo and *Terminalia* sp. surrounded by extensive savanna. The area appears to burn frequently and is comparatively accessible to humans because an ox-cart path passes directly through the region.

Both male tortoises discovered at Ankasakabe had small holes in a rear marginal scute and the gular of one had been cut off. Local villagers had probably kept these tortoises as pets in the past. Captive tortoises often are kept tethered and the gular is removed because it is believed to prevent the tortoise from eating.

Beheta. Beheta was the easternmost locality where tortoises were found and the habitat was roughly 200 ha in size (Figure 2-1). Eighteen tortoises, nine males (298.0-410.0 mm CL), six females (282.0-378.0 mm CL), and three juveniles (116.0-218.0 mm CL) were marked during nearly 164 survey-hours in October and December 1994, and March 1995. The highest observation rate at Beheta occurred during December (0.14 tortoises per survey-hour); this observation rate was similar to that recorded at Cape Sada (0.13 tortoises per survey-hour) over the same period. Although the observation rates at Beheta and Sada in this study were similar, further surveys are needed to determine the population size at Beheta.

The tortoise habitat at Beheta appeared similar to Cape Sada in that it contained bamboo, *Terminalia* spp. and *Bauhinia* sp. However, unlike Sada, stands of shrubs and

bamboo were comparatively sparse. Although vegetative differences were not quantified in this study, brush fires appeared to have degraded the tortoise habitat at Beheta. Villagers mentioned that dry season brush fires are widespread in the region. During the October 1994 visit, a brush fire swept through the area where an adult tortoise had recently been observed. The area was searched during December 1994 surveys and no evidence was found to suggest that the fire killed the tortoise. However, the animal may have been killed, and the carcass scavenged prior to our return. An adult male fire-scarred tortoise and the partial remains of two other adult tortoises were observed in areas that had burned in the past. Although the cause of mortality in these tortoises could not be determined, due to their large size, adult angonoka probably have no natural predators suggesting that fire may have caused the death of these individuals.

One adult female tortoise discovered at Beheta had a hole in a rear marginal scute and had presumably been kept as a pet in the past. Like Ankasakabe, Beheta is comparatively accessible and villagers at Antanandava claim that tortoises are taken from the area on occasion. During a 1992 survey, Juvik et al. (1997) found considerable evidence of bush pig rooting at Beheta. Tracks, rooting, and feces of bush pigs were observed during this study, but no direct evidence of pig predation on eggs or young tortoises was documented.

West Baly Bay

Ambatomainty, Anjaha, Andrafiafaly, Antsahavaky, Antsahamena-south, _Andranolava, and Antsokotsoko._ Bamboo-scrub habitat in these seven areas appeared to be contiguous and probably supports the largest remaining angonoka population. Cloud cover present in the Thematic mapper images of this region did not allow an accurate estimate of the extent of bamboo-scrub habitat in this region. However, it appears to include an area between 4,000-6,000 ha in size. The region contains extensive tracts of bamboo and is relatively inaccessible to humans. The closest human settlements are the villages of Ankoro to the south and Ambarindranahary to the north. A seasonally occupied village exists on the coast at Antsahamena (Figure 2-1).

Twenty-five tortoises were observed in the December and January surveys; ten were adult male (262.0-481.0 mm CL), five were adult female (353.0-395.0 mm CL), and ten were juveniles (53.1-277.0 mm CL). The largest angonoka reported, a male with 481 mm CL, was found at Ambatomainty in the northern portion of the region. The highest observation rate also occurred at Ambatomainty (0.17 tortoises per survey-hour), but comparatively high observation rates also were recorded at Anjaha (0.14 tortoises per survey-hour) and Andrafiafaly (0.11 tortoises per survey-hour). These numbers are similar to those recorded at Cape Sada over the same period (0.11 and 0.24 tortoises per survey-hour in December and January, respectively).

The southern-most localities in this region occurred at Andranolava. Although no tortoises were observed here, tortoise feces were found in three separate locations in the area. Tortoise presence was not confirmed at Antsokotsoko, a large tract of bamboo-scrub habitat that lies between Andranolava and Andrafiafaly. The habitat at Antsokotsoko appears to be contiguous with Andranolava and Andrafiafaly and is similar other sites in the region. Further surveys in this area are needed.

Evidence of brush fires was common throughout the West Baly Bay region. Angonoka were observed using recently burned bamboo-scrub habitat. Two of the 25 tortoises (juveniles with 80 and 140-mm CL, respectively) found during surveys had burn scars. The remains of an adult angonoka were discovered on the beach near the seasonal settlement at Antsahamena. Since local people apparently do not eat angonoka (Durbin et al. 1996), this animal may have been killed and consumed by transient fishermen. Bush pig sign was observed throughout the region, but insufficient time was spent in the area to detect any direct impact of pigs on the tortoise population.

An undescribed species of tick (*Amblyomma* sp.) was observed on five tortoises from Andrafiafaly, Ambatomainty, and Anjaha (L. Durden, pers. com.). Two of the tortoises were adult female, two were adult males, and one was a juvenile with six scute growth rings. Each infected tortoise had from 2-5 ticks attached near the tail and hind legs. This observation represents the first record of an ectoparasite from free ranging *G.*

yniphora and a description of this new tick is in preparation at Georgia Southern University (L. Durden, pers. com).

Betainalika. Betainalika lies approximately 6-km southeast of Andrafiafaly and is separated from the West Baly Bay tortoise habitat by dense deciduous forest and savanna. The bamboo-scrub at Betainalika encompasses approximately 340 ha. The habitat contained only scattered bamboo stalks and appeared to burn frequently. Although the assessment of the habitat in this study was qualitative, Betainalika appeared to have the most extensive fire damage of all the areas visited.

Local villagers repeatedly mentioned that Betainalika had many angonoka. However, during 41 survey-hours in April 1995, only one tortoise was encountered (0.02 tortoise per survey-hour) and neither tracks nor feces were observed. The tortoise observed was a juvenile with 51.9-mm CL and probably was a 1995 hatchling. Despite the low observation rate in this study, the presence of a juvenile tortoise indicated that breeding adults were present in the area. Further surveys in this region are needed to accurately assess the size and status of this population.

Discussion

The tortoise localities identified in this study probably represent at least five separate populations, all of which occur within a 30-km radius of Baly Bay. The "east" and "west" populations are effectively isolated from one another by Baly Bay, the

Andranomavo River, and extensive savanna. The most extensive tract of angonoka habitat occurs west of Baly Bay (including the regions of Ambatomainty, Anjaha, Andrafiafaly, Antsahavaky, Antsahamena-south, Andranolava, and Antsokotsoko). This area is approximately 4,000-6,000 ha in size and probably contains the largest angonoka population. More intensive tortoise surveys are needed in this region to determine the population size, and the area should be evaluated to determine the precise extent and quality of the tortoise habitat. The Betainalika region also occurs west of Baly Bay and probably represents a separate population. Betainalika is much smaller than the west Baly Bay region and appeared to contain low tortoise densities. However, further surveys in this region also are warranted.

The three angonoka populations east of Baly Bay, Cape Sada, Beheta, and Ankasakabe, occur on small tracts of habitat (<200 ha in size) and are separated by extensive savanna. Cape Sada is only about 150 ha in size and hosts a population of 99 tortoises. Beheta is roughly the same size as Cape Sada and although the habitat appears somewhat degraded by fire, similar observation rates suggest that the populations may be similar in size. Tortoise habitat at Ankasakabe is extremely restricted and this angonoka population is undoubtedly very small. The observation of tracks of a juvenile tortoise at Ankasakabe indicates that angonoka are able to reproduce successfully in small habitat fragments. However, it is not known whether recruitment into the breeding population is occurring in this limited habitat.

The tortoise density on Cape Sada (0.66 tortoises per ha) appears low when compared to other dry scrub-forest tortoises. For example, the density of Hermann's tortoise (*Testudo hermanni*) at a site in northeastern Spain was nearly 11 tortoises/ha (Mascort 1997) and densities of 3-4 tortoises/ha have been reported for the Chaco tortoise (*Geochelone chilensis*) in Argentina (Waller and Micucci 1997). Radiated tortoises (*Geochelone radiata*) in southern Madagascar inhabit a much drier climate than angonoka; however, estimates of 7-15 tortoises/ha have been reported for this species (R. Lewis, pers. com.). The apparent low tortoise density at Cape Sada may reflect the effects of past harvest, poor habitat quality, or low survivorship. Comparative studies at other angonoka populations are needed to determine whether densities are similar in other patches of bamboo-scrub habitat.

Juvenile tortoises were found in all areas surveyed, indicating that successful reproduction is occurring throughout the range of the angonoka. Although African bush pigs are known to have destroyed one tortoise nest after this study (Pedrono 1996), some nests are clearly surviving to produce hatchlings. However, a large mammal such as an African bush pig may have killed at least two large juvenile tortoises on Cape Sada. Bush pig predation may have a significant effect on recruitment, particularly if pigs prey heavily on juvenile tortoises that are too large to be consumed by native predators. Additional dead juveniles observed on Cape Sada in this study, and an apparent lack of intermediate sized tortoises, may indicate low juvenile survivorship in this population.

Brush fires probably pose the most serious threat to remaining angonoka populations. The 1995 fire on Cape Sada confirmed that brush fires kill angonoka and it seems likely that frequent brush fires also affect the structure of the bamboo-scrub habitat. Although no quantitative data were collected, the bamboo-scrub at Beheta, Ankasakabe, and Betainalika appeared badly degraded by brush fires. Bamboo thickets at these sites were structurally quite different than at other areas. Bamboo was notably sparse and dense vines had encroached in some areas.

In order to assess the impact of anthropogenic fires on the bamboo-scrub ecosystem, the role of natural fire in the region must be determined. Paleoecological investigations have shown that brush fires occurred in western Madagascar prior to human settlement (Burney 1997). However, the frequency of anthropogenic dry season fires is probably quite different from that of natural fires. Given the highly seasonal rainfall pattern in the region, it is unlikely that lightning fires would occur in the dry season (when most anthropogenic fires occur). Furthermore, lightning induced wet season fires would probably be less catastrophic than dry season fires because the fuels would be more moist. Research is needed to determine the direct effects of fire (both anthropogenic and natural) on the bamboo-scrub ecosystem.

In addition to evaluating the effects of brush fires on the angonoka, it also will be important to determine the effects of cattle and African bush pigs on the bamboo-scrub habitat. In a desert tortoise (*Gopherus agassizii*) population, tortoises were in direct

competition with cattle for food (Avery and Neibergs 1997). Cattle were responsible for degrading Chaco tortoise (*Geochelone chilensis*) habitat by grazing new shoots of shrubs following anthropogenic fires (Waller and Micucci 1997). Overlap in diet between feral pigs (*Sus scrofa*) and giant tortoises (*Geochelone nigra*) was documented on Isla Santiago in the Galapagos, although direct competition between the two species was not confirmed (Coblentz and Baber 1987). Considerable pig rooting activity was observed in all regions surveyed in this study. Additional information is needed to evaluate the impacts of cattle and bush pigs on bamboo-scrub habitat.

Most of the remaining angonoka populations are very remote and collection of tortoises does not appear to be a threat at this time. On a local level, tortoises may occasionally be kept as pets, but community education efforts have resulted in the donation of captive animals to the breeding program (Curl 1986b; Reid et al. 1989), and others have apparently escaped or been released back into the wild (e.g., Beheta and Ankasakabe). However, the theft of 75 angonoka from the captive-breeding center at Ampijoroa in 1996 demonstrates a demand for this rare species in the international pet trade (Webster 1997). Declaration of the Baly Bay region as a National Park by the Malagasy government is imminent; however, wild populations still may be vulnerable to illegal collection in the future. The removal of adult tortoises from any of the wild populations could have catastrophic effects. The apparent low survivorship of juvenile angonoka coupled with a slow rate of development to sexual maturity could severely

limit the capacity of a population to recover from the loss of adult tortoises (see Congdon et al. 1993). It may be necessary to use guards to protect the most accessible angonoka populations (e.g., Cape Sada and Beheta).

The angonoka is vulnerable to extinction in the wild primarily because of its extremely limited geographic distribution. The remaining populations are small, isolated, and all occur within only a 30 km radius of Baly Bay. Although juveniles were found in all populations, the population structure at Cape Sada indicates that recruitment into the breeding population may be low. A catastrophic event such as disease or severe weather could cause extinction of some or all populations. Augmentation of the Cape Sada angonoka population with captive born juveniles is not warranted at this time. However, repatriation (release of individuals of a species into an area formerly occupied by that species) may be worthwhile in other areas. It is of critical importance to protect and manage all wild angonoka populations in order to preserve the species.

Table 2-1. Number of wild angonoka (*Geochelone yniphora*) observed during regional surveys around Baly Bay in western Madagascar from 1993 through 1995. *= Although no tortoises were seen, tracks and/or feces were observed.

LOCATION	SURVEY DATES	MALES	FEMALES	JUVENILES	TOTAL
East Baly Bay					
Cape Sada	6 October 1993 – 24 June 1995	14	27	58	99
Beheta	11-12 October 1994; 11-15 December 1994; 17-19 March 1995; 22 May 1995	9	6	3	18
Ankasakabe	20 March 1995; 8-9 April 1995	2	0	0	2
		25	33	61	119
West Baly Bay					
Ambatomainty	3, 4 and 5 January 1995	2	2	0	4
Andrafiafaly	21, 22, and 27 December 1994	3	1	3	7
Andranolava*	26 December 1994	0	0	0	0
Anjaha	23 and 31 December, 1994; 2, 4, and 7, January 1995	4	2	6	12
Antsahavaky	24 December 1994	1	0	1	2
Antsokotsoko	26 and 28 December 1994; 21 April 1995	0	0	0	0
Antsahanena- South*	6 January 1995	0	0	0	0
Betainalika	17-21 April 1995	0	0	1	1
		10	5	11	26

Table 2-2. Observation rates of angonoka (*Geochelone yniphora*) during 1994-1995 field surveys in western Madagascar. Rates were calculated as the number of tortoises observed per person/hour of survey. [†]Only December and January survey results are presented here for comparative purposes. *Tortoise tracks and/or feces observed.

LOCALITY	DATES	PERSON HOURS	NUMBER OF TORTOISES OBSERVED	OBSERVATION RATE
East Baly Bay				
Cape Sada[†]	Dec	32.0	4	0.13
	Jan	66.8	19	0.28
Beheta	Oct	31.5	3	0.10
	Dec	99.8	14	0.14
	Mar	32.5	2	0.06
Ankasakabe	Apr	32.5	2	0.06
West Baly Bay				
Ambatomainty	Dec-Jan	24.0	4	0.17
Anjaha	Dec-Jan	61.0	8	0.13
Andrafiafaly	Dec-Jan	63.0	7	0.11
Antsahavaky	Dec-Jan	28.0	1	0.04
Betainalika	Apr	49.0	1	0.02
Andranolava	Dec-Jan	8.8	0	0.00*
Antsokotsoko	Dec-Jan	22.2	0	0.00
Antsahamena-S	Dec-Jan	21.0	0	0.00*

Table 2-3. Mean carapace length of wild caught angonoka (*Geochelone yniphora*) in western Madagascar. Measurements are in millimeters. *Includes Ambatomainty, Anjaha, Andrafiafaly, and Antsahavaky.

LOCATION	SEX/LIFE STAGE	*N*	MEAN	RANGE	SD
East Baly Bay					
Cape Sada	Males	14	409.6	282.0 - 456.0	45.0
	Females	26	361.8	285.0 - 405.0	29.0
	Juveniles	42	120.9	44.9 - 310.0	79.6
	Hatchlings	16	47.2	43.5 - 52.0	3.0
Beheta	Males	9	360.2	298.0 - 410.0	41.5
	Females	6	342.2	282.0 - 378.0	39.7
	Juveniles	3	168.7	116.0 - 218.0	51.1
Ankasakabe	Males	2	414.0	396.0 - 432.0	25.5
West Baly Bay					
Western areas*	Males	10	405.0	262.0 – 481.0	61.1
	Females	5	375.2	353.0 – 395.0	16.3
	Juveniles	10	141.8	53.1 – 277.0	62.5
Betainalika	Juveniles	1	51.9		

Figure 2-1. Angonoka tortoise (*Geochelone yniphora*) localities in the Baly Bay, region of western Madagascar. Locality information is based on observations of tortoises and/or the presence of tortoise tracks or feces during 1993-94 field surveys.
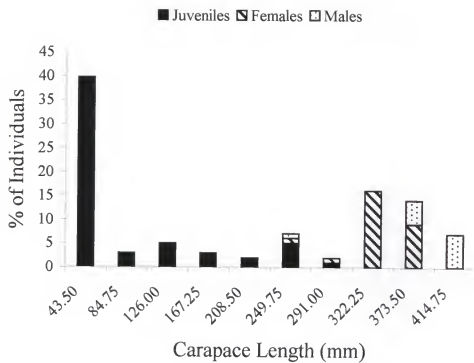
Figure 2-2. Size class distribution of the Cape Sada angonoka tortoise (*Geochelone yniphora*) population (n=98).
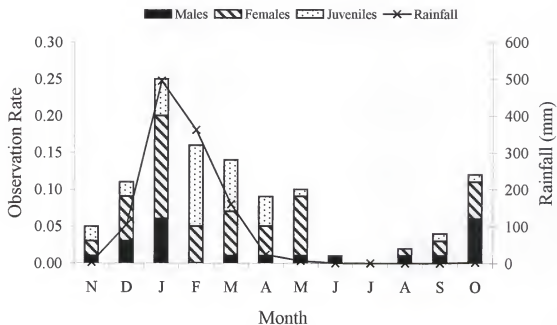
Figure 2-3. Mean monthly observation rates for angonoka tortoises (*Geochelone yniphora*) as related to monthly rainfall totals at Cape Sada, Madagascar. Observation rates were calculated as the number of tortoises observed per person-hour of survey.
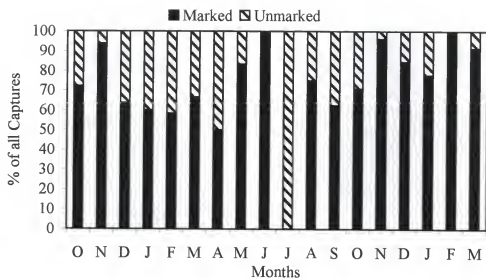
Figure 2-4. The ratio of marked to unmarked angonoka tortoises (*Geochelone yniphora*) observed at Cape Sada, Madagascar. Data were collected from October 1993 through March 1995.

CHAPTER 3
HOME RANGE AND MICROHABITAT USE

Introduction

Little is known of the habitat requirements of the angonoka. All records for this
species indicate that it is restricted to bamboo-scrub habitat in the Baly Bay region of
western Madagascar (Siebenrock 1903; Juvik et al. 1981; Curl et al. 1985; Reid 1989,
1990a, 1990b). Today there are less than 7,000 ha of bamboo-scrub remaining and the
habitat is fragmented and surrounded by extensive savanna (Chapter 2). In order to
protect and manage existing angonoka populations given the limited habitat, it is critical
to identify components of the bamboo-scrub ecosystem that are important to these
tortoises. It also is critical to quantify the spatial needs and dispersal behavior of
individual tortoises. Home range is the area used by an animal during its normal
activities of food gathering, mating, and caring for young (Seton 1909; Burt 1943; Stickel
1954) and is an important measure of the spatial needs. The most common methods of
estimating home range size are reviewed below.

The objectives of this part of the study were to determine home range size and
patterns of microhabitat use in adult and juvenile angonoka. I examined (1) variation in
home range size among males, females, and juveniles; (2) differences in home range size

across seasons; (3) differences in microhabitat use between male, female, and immature

tortoises; and (4) seasonal differences in microhabitat use.

Review of Home Range Methods

Most early methods for estimating home range were developed for small mammals

and used observations based on sight records or mark/recapture (Blair 1940; Burt 1943;

Dalke 1942; Hayne 1949; Mohr 1947). Sight records often were opportunistic and these

studies generally had very low sample sizes. Trapping methods used in mark/recapture

studies relied on the unlikely assumption that traps within a home range were equally

successful and that animals did not move beyond the trapping grid. The development of

radio-telemetry in the late 1960s allowed researchers to monitor animal movements more

closely and to directly observe animal behavior (Adams 1965).

Numerous methods for calculating home range have been described since the

1940s (see Worton 1987). Nonstatistical methods, such as polygon estimates, give the

extent of an animal's home range. The three most commonly used polygon methods are

minimum area (MA), minimum convex polygon (MCP), and modified minimum area

(MMA). In the MA method, straight lines connect observation points and the area

enclosed by the polygon is measured (Dalke 1942; Stickel 1954; Southwood 1966). This

method has not been clearly defined and the shape of the polygon depends on the order in

which the points are connected (Jennrich and Turner 1969). MCP is simply the smallest

possible convex polygon containing all of the observation points. This method is very

sensitive to movements on the periphery of the animal's home range, regardless of the frequency with which that area is visited by the animal. A further limitation to this method is that large areas of land that are not visited by the animal can be included in the polygon. The MMA method is a modification of the MCP method that was designed to eliminate areas within the polygon where an animal does not go. Any points that are further than one-fourth the range length (the distance between the two farthest observation points) from any other point are considered forays outside the animal's home range and are excluded from the polygon.

Polygon methods give no information about the internal anatomy of the home range. Most animals do not use their entire range with equal intensity (Hayne 1949); they tend to occupy particular areas within their home range (e.g., dens, nest sites, and limited resources) with greater frequency than other areas. Areas of concentrated use are called centers of activity or core areas (Samuel et al. 1985). Statistical home range models attempt to measure the intensity of use within the home range. These models define home range as the area of the smallest subregion, which accounts for some proportion (usually 95 %), p, of its total utilization.

The earliest statistical models include recapture radius/standard circle and the covariance matrix method (Harrison 1958; Dice and Clark 1953). The recapture radius method defines a "standard diameter" as twice the square root of the mean square of all distances between observation points and the geometric center of activity. A circle based on this diameter is called a "standard circle" and contains 68.26 % of all observations.

The covariance matrix method is a modification of the recapture radius method that is designed to measure non-circular home ranges (Calhoun and Casby 1958; Jennrich and Turner 1969). This model assumes that the utilization distribution is bivariate normal. The most heavily used areas are bounded by concentric density ellipses that account for a proportion of the animal's total use of its home range. Circular and the covariance matrix methods have little biological significance because home ranges rarely are circular or elliptical.

Recent utilization distribution (UD) models calculate home range as a discrete or continuous function that represents the intensity with which an animal uses points in its habitat (Siniff and Tester 1965; Adams and Davis 1967; Voight and Tinline 1980; Anderson 1982; Don and Rennolls 1983; Worton 1987). These methods, unlike circular or elliptical models, carry no assumption about the form of the home range. UDs are presented graphically as contour lines, each of which is a set of points where the probability of occurrence is constant. For example, the kernel area (KA) utilization distribution method (Worton 1989), uses a probability density function, called a *kernel*. A kernel is placed over each observation point and an estimator is constructed by adding the n components (random sample of n independent points). Where there is a concentration of points, the kernel estimate has a higher density than where there are few points. A smoothing parameter, h, is used to control the amount of variation in each component of the estimate. A large h obscures all but the most prominent feature, whereas a small h retains the fine detail of the data.

As yet there is no ideal measure of home range. MCP has historical significance (Stickel 1954; Rose 1982) and has been found to be more comparable between species and individuals than other measures (Mohr 1947). The method is simple to use and is based on actual observations of an animal. Sample size bias can be removed with adequate sampling; however, the problem of incorporating areas not used by the animal is more difficult to resolve. MMA does not completely resolve the problem because the use of one-fourth of the range length to exclude outlying points is arbitrary.

Recapture radius/standard circle and bivariate normal methods are unreliable because they assume a normal distribution of the data. This assumption rarely is met; home ranges often are linear or irregularly shaped. Animal movements are not random and weighted measures of centers of activity probably present a more realistic measure of spatial patterns. The most robust estimators of UD are methods such as harmonic mean and kernel area, which do not make assumptions about the underlying distribution of the data.

In this study, I used both MCP and kernal area (KA) method for estimating home range size. MCP method was used so that the results would be comparable to those of other studies. Also, I felt I could resolve the problem of sample bias in this method by obtaining a large number of sample points for each individual. KA method was used to obtain a more accurate representation of the functional home range of the angonoka and to depict areas of concentrated use within the home range.

Methods

Thirteen tortoises (3 males, 5 females, and 5 juveniles with 8-10 scute growth rings) were radio-instrumented and tracked for periods ranging from 121 to 630 days (Table 3-1). Adult tortoises were fitted with SB-2 module transmitters and juveniles with smaller SM-1H modules that weighed 30 g and 7 g, respectively (AVM Instrument Company, Ltd., Livermore, CA). Transmitters (including batteries) weighed less than 1 % of the tortoises body weight and were attached to the posterior costal scutes of the tortoise with PC-11 Epoxy Paste (Protective Coating Co., Allentown, PA).

The tortoises were located by direct observation using an LA-12 receiver (AVM Instrument Company, Ltd., Livermore, CA). Each animal was located 7 mornings (between 0600-1030 hrs) and 7 afternoons (between 1430-1800 hrs) per month, weather permitting. At each location, the time, weather, air and substrate temperature, relative humidity, and microhabitat type (scrub-shrub, bamboo, grass, or open) were recorded.

The scrub-shrub microhabitat contained shrubs less than 2 m in height with scattered grasses and sedges in the ground cover. The most common shrub species were *Bauhinia* sp. and *Terminalia* spp. The bamboo microhabitat consisted of dense thickets of bamboo (*Perrierbambos madagascariensis*) with a few shrubs and satrana palms (*Bismarkia nobilis*), but ground cover vegetation was rarely present. Small grassy areas, generally less than 5 m² in area, were classified as "grass" microhabitat. These areas contained savanna grasses including *Aristida* sp., *Eragrostis* sp., and *Heteropogon contortus* and a variety of sedges, although they did not fit the traditional definition of

savanna (Koechlin 1972). Open unvegetated patches (typically <3 m^2 in area) with an igneous rock substrate were considered a fourth microhabitat. These small areas typically were found within the scrub-shrub and grass microhabitats.

A 50-m^2 grid was created across most of Cape Sada. Tortoise locations were marked with colored flagging, numbered consecutively, and the distance and compass bearing to the nearest grid point taken. If no transect or grid point was available, localities were determined with an Ensign XL Global Positioning System (Trimble Navigation, Sunnyvale, CA).

Minimum convex polygon (MCP) (Mohr 1947) and kernel area (KA) (Worton 1989) methods were used to estimate home range size. Analyses were carried out using the computer program Ranges V (Kenward and Hodder 1996). MCPs were based on 100 % of the fixes and KAs were calculated using 95 % contours. Least-squares cross-validation was used to choose the optimum smoothing factors in KA analysis (Silverman 1986; Kenward and Hodder 1996).

Sampling periods were grouped into two seasons for analysis (November - April = wet season; May - October = dry season). A Wilcoxon paired-difference test was used to examine wet and dry season effects on home range size and a Kruskal-Wallis test was used to test for differences in home range size between males, females, and juveniles in both wet and dry season.

A 1990 thematic mapper satellite image (Juvik et al. 1997) was used to quantify the extent of the various microhabitat types on Cape Sada. Areas were estimated using a

polar planimeter. A Chi-squared goodness-of-fit test was used to determine whether there was a difference between observed and expected microhabitat use, based on habitat availability.

Analysis of categorical data (percent of observations by sex, season, and microhabitat) was carried out using analysis of covariance (PROC GLM) (SAS Institute, Inc. 1992). If significant treatment effects were detected, Tukey's studentized range (HSD) test was used to determine where the differences occurred (Kushner and De Maio 1980). Scrub-shrub was excluded from the microhabitat analysis because it accounted for most of the available habitat and interactions would be difficult to distinguish.

Results

Home Range. Home range maps are presented in Appendix A. There was considerable variation in home range size among individual tortoises (Table 3-2). However, several general patterns were evident. Wet season home ranges were significantly larger than dry season home ranges with both MCP and KA method (MCP: t= 2.70; df= 12; P= 0.01; KA: t= 2.88; df= 12; P= 0.02). MCP values were greater than KA values in both wet and dry season because KA estimates were based on only 95 % of observations and excluded areas not visited by the tortoise. Because KA probably best reflected actual home range size, only comparisons among KA values are discussed below.

Wet season home range areas were significantly different among the sex/life

stages (H= 9.33; *P*<0.01). The average size of juveniles tracked in this study was 167

mm CL as compared to 427 and 362 mm CL in adult males and females, respectively. In

general, body size is related to home range size, because larger animals often need to

forage farther to meet their energy requirements than do small animals (McNab 1963),

although other factors such as metabolism, feeding strategy, and probability of predation

(Weatherby 1995) also may influence home range size. These factors may explain the

difference in home range size between adult and juvenile angonoka. However, immature

tortoises of other species occasionally use larger home ranges than adults because they

conduct long distance dispersal movements (Auffenberg and Iverson 1979; Aguirre et al.

1984; Diemer 1992). The juveniles followed in this study did not exhibit this behavior.

In adult angonoka, behavior rather than body size probably best explains the variation in

home range size between the sexes (Figure 3-1). Males in this study were more nomadic

than females and traveled over large areas, possibly in search of mates.

No significant difference in dry season home ranges between the sex/life stages

was detected (H= 0.54; *P*>0.10). These results may be an artifact of the small sample

size in this study because the mean juvenile home range size (0.6 ha) was much smaller

than that of adult males (6.6 ha) and females (3.6 ha).

There was little overlap among home ranges of adult males and females in the dry

season (Figure 3-2). During the wet season, the home range of adult males expanded to

encompass all or portions of that of females, but male ranges only intersected at the

periphery (Figure 3-3). The apparent lack of overlap among adult males may indicate that angonoka exhibit a dominance hierarchy among males (Harless 1979). However, more data are needed in order to get a clear picture of the spatial distribution of all tortoises in this population. The apparent low tortoise density on Cape Sada may influence spatial distribution. Home range areas of 5 juveniles followed in this study did not overlap in either the dry or the wet season (Figure 3-4 and 3-5). Again, this may be an artifact of the low tortoise density on Cape Sada. However, the tortoises radio-tracked in this study represent only small fraction of those present on Cape Sada. The home ranges of the individuals in this study may have overlapped with tortoises that were not instrumented.

Microhabitat Use. Scrub-shrub is the predominant microhabitat type on Cape Sada and occupies approximately 59% of the peninsula. The bamboo microhabitat occurs primarily on the highest elevations of the Cape and covers approximately 28% of the study area. Patches of grass occupy approximately 4%. Open microhabitat was difficult to distinguish on the satellite image because it typically occurs in patches only a few square meters in size within the scrub-shrub or grass. However, open areas probably occupy about 4% of the site. Komanga forest covers approximately 5% of the peninsula.

Tortoises were most often observed in scrub-shrub, (2070 of 3149 observations; 65.7 %) followed by bamboo (819; 26.0 %), grass (164; 5.2 %) and open habitat (96; 3.1 %). Radio-instrumented angonoka were never encountered in the komanga forest. Angonoka on Cape Sada used microhabitats relative to their availability (χ^2= 6.26; df= 4;

$P= 0.20$); however, season appeared to have an effect on microhabitat selection ($F= 3.21$, df$= 2$, $P= 0.0447$) (Table 3-3). All angonoka used the open microhabitat significantly more often in wet season than in dry season, while angonoka were observed significantly more often in the grass microhabitat in dry season than in wet season (Table 3-4).

Although no significant difference in microhabitat use between male, female and juvenile tortoises was detected ($F=0.82$; df$= 4$; $P=0.1390$), when the data were examined by month (Figures 3-6, 3-7, and 3-8), it appeared that adults of both sexes used bamboo more often in the late dry season (September and October) and early wet season (November). Juvenile tortoises appeared to use the bamboo microhabitat more frequently during wet season months than during the dry season months (Figure 3-8).

Discussion

Despite a great deal of individual variability, seasonal differences in adult home range size were observed in this study. Home range areas were larger in the wet season, when food and water were plentiful, than in the dry season when these resources were limited. Tortoises were most often observed in scrub-shrub (SS) and bamboo (BA), the most common microhabitat types on Cape Sada. However, the use of other microhabitats differed among seasons. For example, angonoka were encountered more frequently in the open microhabitat during the wet season, because in general tortoises were more vagrant in wet season when environmental temperatures were high and moisture was not limited. Tortoises were observed feeding on the few herbs and grasses available in open

areas during the wet season and often were observed passing through these areas. In the dry season, angonoka used the patches of grass more often than in the wet season. This difference may relate to the tortoise's ability to maintain an optimal body temperature by sheltering under grasses during the cool, but sunny, dry season. Giant tortoises (*Dipsochelys dussumieri*) and box turtles (*Terrapene carolina*) also exhibit seasonal shifts in habitat use related to thermoregulation (Stickel 1950; Reagan 1974; Swingland and Lessells 1978; Gibson and Hamilton 1983; Dodd et al. 1994).

Although no statistical difference in microhabitat use was detected between adult male, adult female, and juvenile angonoka in this study, adults appeared to use bamboo more often in October and November (late dry season). This coincides with breeding activity (Chapter 4) and may indicate that the bamboo habitat is important as a staging area for courtship. Differences in habitat use may exist between different angonoka populations. For example, female angonoka in a population west of Baly Bay used grass more often in the wet season than in the dry season. Females in the west Baly Bay population often nested in grass habitat (M. Pedrono, pers. com.). The grass habitat used by female angonoka in the western population was more similar to true savanna. Female tortoises on Cape Sada tended to nest in the scrub-shrub or bamboo microhabitat, and only rarely in open, unvegetated areas (Chapter 4).

The findings of this study regarding seasonal shifts in microhabitat use by the angonoka underscore the importance of maintaining the diversity of vegetation types within the bamboo-scrub ecosystem. Furthermore, grasses and vines in frequently

burned angonoka habitat replace bamboo and shrubs, the two primary components of this ecosystem. The reduction of these components of the ecosystem may severely reduce the suitability of the habitat for tortoises. The loss of bamboo and shrubs probably results in an increase in air and substrate temperatures and a decrease in relative humidity.

The role, if any, of natural bush fires in the maintenance of the bamboo-scrub habitat of the angonoka is not understood. Only a few studies have documented the effects of fire on tortoise species and their habitat. Natural fires ignited by lightning promote species diversity in the sandhill habitat of the gopher tortoise (*Gopherus polyphemus*) in the southeastern United States (Laessle 1958). Gopher tortoises have adapted to a fire-maintained ecosystem by using subterranean burrows for refuge. The evergreen shrub/grassland (renosterveld) habitat of the South African geometric tortoise (*Psammobates geometricus*) also is fire-maintained (Baard 1995). However, frequent wildfires degrade the renosterveld ecosystem and unseasonable fires can kill adult and juvenile tortoises (Baard 1993). Catastrophic effects of anthropogenic fires also have been documented in Hermann's tortoise (*Testudo hermanni*) in Greece (Hailey and Goutner 1991).

In western Madagascar, natural fires would be expected to take place in the wet season, when lightning storms occur. However, anthropogenic fires typically are set in the dry season and probably function quite differently than natural fires. Natural fires occur sporadically and undoubtedly with much lower frequency than manmade brush fires. Furthermore, dry season fires are probably more intense than wet season fires

because fuel loads are greater. Therefore, intense dry season fires could be expected to have a great impact on tortoises. It seems likely that manmade fires, by altering the bamboo-scrub habitat or killing tortoises outright, are a major threat to remaining angonoka populations.

Home ranges of adult angonoka overlapped considerably, particularly during the wet season. However, the ranges of the three adult males only overlapped at the periphery, and it appears that male angonoka may exhibit a dominance hierarchy. More information is needed regarding the social structure of angonoka populations. Questions concerning spatial needs of the angonoka are particularly important with only 4,000-6,000 ha of bamboo-scrub habitat remaining. Long-term monitoring of the Cape Sada population is needed to determine whether the population is increasing (despite high juvenile mortality), decreasing, or stable (at equilibrium density).

As mentioned previously, angonoka are being bred in captivity with the intent of augmenting wild populations. I believe that habitat protection and restoration, rather than augmentation, should be a conservation priority for this species at this time. However, unoccupied tracts of bamboo-scrub may be suitable for reintroduction of captive-born tortoises in the future. In the meantime, future research should focus on identifying differences in the microclimate of scrub-shrub, bamboo thickets, grass and open areas that may be important to the angonoka.

Table 3-1. Radiotracking information for 13 angonoka (*Geochelone yniphora*) on Cape Sada, Madagascar. Data were collected from October 1993 through June 1995.

TORTOISE NO.	CARAPACE LENGTH (MM)	TRACKING INTERVAL	NUMBER OF RECORDS
Juveniles:			
42	173	2/95 – 6/95	63
44	168	11/93 – 6/95	256
51	156	10/93 – 6/95	282
83	167	10/94 – 6/95	130
88	172	10/94 – 6/95	121
Mean:	167		
Males:			
7	430	10/93 – 6/95	278
13	398	10/93 – 6/95	288
54	454	12/93 – 6/95	229
Mean:	427		
Females:			
1	376	10/93 – 6/95	303
3	329	10/93 – 6/95	301
9	344	10/93 – 6/95	285
12	361	10/93 – 6/95	292
19	399	11/93 – 6/95	264
Mean:	362		

Table 3-2. Mean home range size (in hectares) of 13 radio-instrumented angonoka (*Geochelone yniphora*) on Cape Sada, Madagascar. Home range size was estimated using minimum convex polygon method (MCP) (Mohr, 1947) and kernel area (KA) (Worton, 1989). Data were grouped into two seasons for analysis (November - April = wet season; May - October = dry season). For each category the mean is followed by ± 1 SD and the range.

SEX/LIFE STAGE	DRY SEASON		WET SEASON	
	MCP	KA	MCP	KA
Juveniles (N=5)	1.4 ± 1.1 (0.1 – 2.5)	0.6 ± 0.5 (0.0 – 1.3)	2.2 ± 1.5 (1.0 – 4.8)	1.8 ± 1.8 (0.6 – 5.0)
Males (N=3)	9.2 ± 4.6 (4.6 – 13.9)	6.6 ± 4.5 (1.4 – 9.8)	38.5 ± 7.0 (31.6 – 45.5)	21.1± 6.4 (6.4 – 28.4)
Females (N=5)	8.7 ± 9.8 (1.0 – 25.6)	3.6 ± 5.0 (0.5 – 12.5)	17.7 ± 18.2 (10.6 – 42.0)	12.2 ± 9.4 (4.7 – 28.5)

Table 3-3. Analysis of Covariance of the effects of season and habitat where a tortoise was observed, and sex/life stage (males, females, and juveniles) on percent of observations of angonoka tortoises on Cape Sada, Madagascar. *$P<0.05$ indicates values that were not uniformly distributed.

COMPARISON	DF	F	P
Habitat	2	38.42	0.0001*
Season	1	0.03	0.8684
Sex	2	0.82	0.4436
Habitat*Season	2	3.21	0.0447*
Habitat*Sex	4	1.78	0.1390

Table 3-4. Results of Tukey's studentized range (HSD) test comparing mean percent of observations of angonoka tortoises by season and habitat type (N=18) on Cape Sada, Madagascar. Habitat types included bamboo (BA), open (OP) and grass (GS). MSD= minimum significant difference, *= significantly different ($P< 0.05$).

HABITAT	SEASON	MEAN	SD	DIFFERENCE	MSD
BA	Dry	21.77	19.20	6.08	11.773
BA	Wet	27.86	15.34		11.773
OP*	Dry	1.55	2.63	2.24	1.864
OP	Wet	3.79	2.87		1.864
GS*	Dry	10.04	13.71	7.23	6.630
GS	Wet	2.81	1.89		6.630
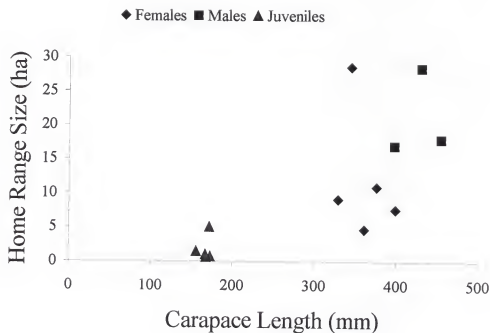
Figure 3-1. Wet season (November - April) home range size as related to carapace length (in mm) for 13 angonoka tortoises (*Geochelone yniphora*) at Cape Sada, Madagascar. Home range was calculated using Kernal Area method (Worton, 1989).
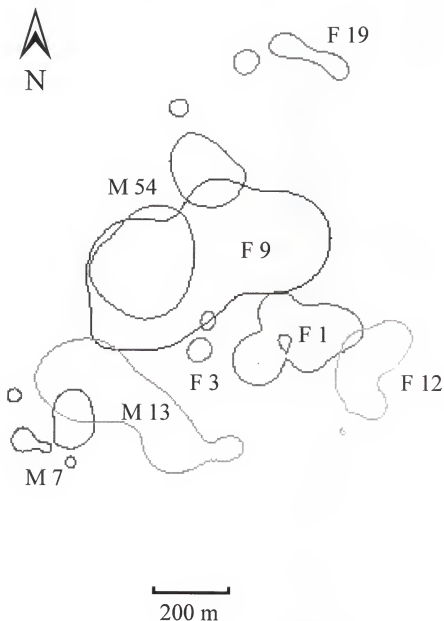
Figure 3-2. The spatial distribution of dry season home ranges for eight adult angonoka (*Geochelone yniphora*) at Cape Sada, Madagascar. Dry season extended from May through October. Home ranges were calculated using the kernel area method (Worton 1987).
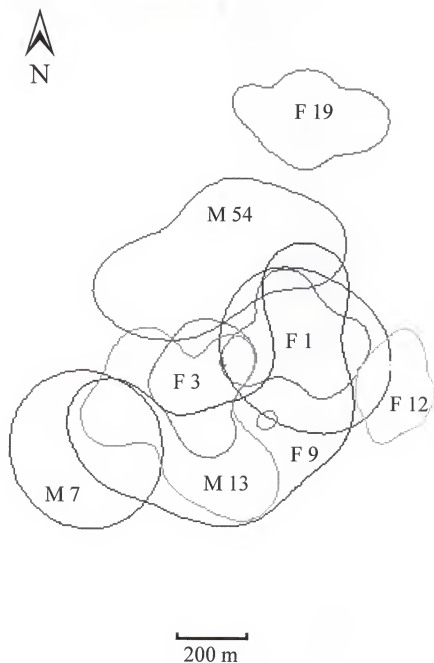
Figure 3-3. Spatial distribution of wet season home ranges for eight adult angonoka (*Geochelone yniphora*) at Cape Sada, Madagascar. Wet season extended from November through April. Home ranges were calculated using the kernel area method (Worton 1987).
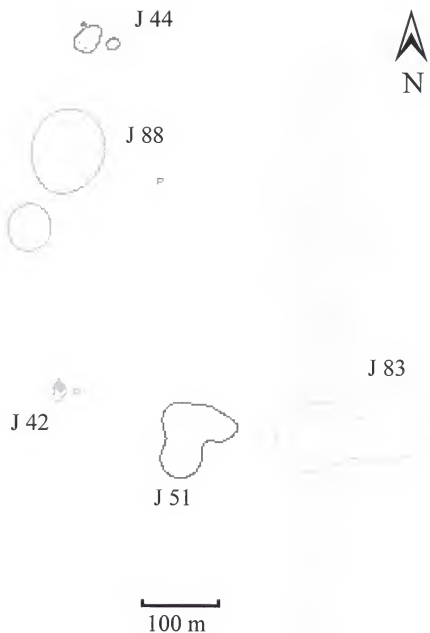
Figure 3-4. Spatial distribution of dry season home ranges for five juvenile angonoka (*Geochelone yniphora*) at Cape Sada, Madagascar. Dry season extended from May through October. Home ranges were calculated using the kernel area method (Worton 1987).

Figure 3-5. Spatial distribution of wet season home ranges for five juvenile angonoka (*Geochelone yniphora*) at Cape Sada, Madagascar. Wet season extended from November through April. Home ranges were calculated using the kernel area method (Worton 1987).
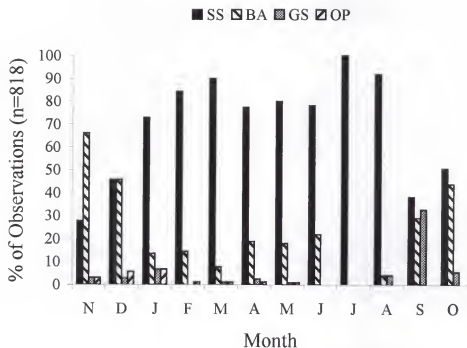
Figure 3-6. Monthly patterns in microhabitat use in three adult male angonoka tortoises (*Geochelone yniphora*) at Cape Sada, Madagascar. Numbers represent the percent of observations of radio-instrumented tortoises in scrub-shrub (SS), bamboo (BA), grass (GS), and open (OP) microhabitats. Data were collected from October 1993 through June 1995.
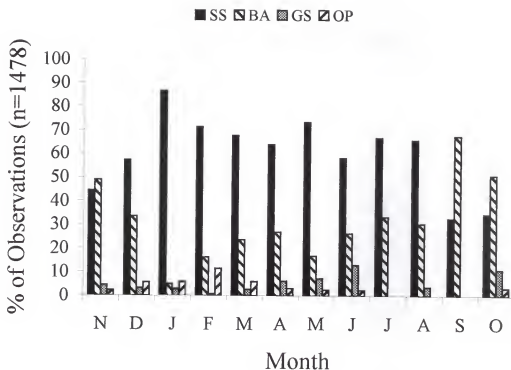
Figure 3-7. Monthly patterns in microhabitat use in five adult female angonoka tortoises (*Geochelone yniphora*) at Cape Sada, Madagascar. Numbers represent the percent of observations of radio-instrumented tortoises in scrub-shrub (SS), bamboo (BA), grass (GS), and open (OP) microhabitats. Data were collected from October 1993 through June 1995.
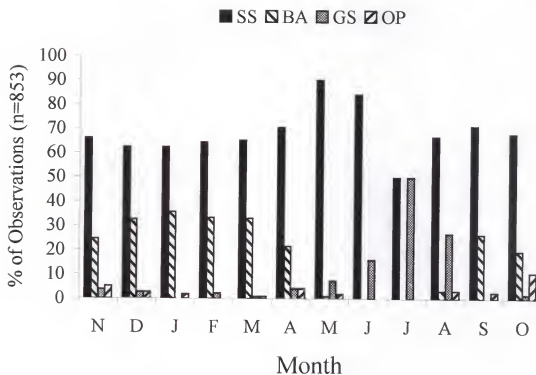
Figure 3-8. Monthly patterns in microhabitat use in five juvenile angonoka tortoises (*Geochelone yniphora*) at Cape Sada, Madagascar. Numbers represent the percent of observations of radio-instrumented tortoises in scrub-shrub (SS), bamboo (BA), grass (GS), and open (OP) microhabitats. Data were collected from October 1993 through June 1995.

CHAPTER 4
BEHAVIOR AND ACTIVITY PATTERNS

Introduction

Activity patterns of terrestrial turtles are directly related to environmental

temperature and moisture (Gourley 1979). Temperature exerts a strong influence on

activity in a temperate climate (Oliver 1955; Carpenter 1957; Sexton 1959; Gibbons

1970; Douglass and Layne 1978; Lovich 1988; Lovich 1990; Lovich et al. 1992; Gibbons

et al. 1990; Claussen et al. 1991; Mushinsky and Wilson 1992; Dodd et al. 1994),

whereas in a tropical climate, moisture often has a strong influence on activity

(Woodbury and Hardy 1948; Rose and Judd 1982; Swingland and Lessells 1979). In the

tropical climate of western Madagascar, activity of the angonoka appeared to be closely

tied to seasonal rainfall (Juvik et al. 1981). More than 90 % of all precipitation in the

region occurs in the summer, from November through March (Donque 1972). The small

number of observations of angonoka during winter surveys (May through October)

supported the assumption that this species was dormant during the dry season (Juvik et al.

1981; Juvik et al. 1997). However, seasonal activity patterns for this species had not

been examined in detail.

Past descriptions of the behavior of angonoka were based on anecdotal

observations of wild tortoises (Juvik et al. 1981; Juvik et al. 1997) and on observations of

captive individuals (McKeown et al. 1982; Reid 1995). Mating and nesting had never been observed in the wild, and it was thought that population levels were depleted to a level where little or no reproduction was taking place (Juvik et al. 1981; Burke 1990). In captivity, male angonoka exhibited considerable agonistic behavior during courtship (McKeown et al. 1982; D. Reid, pers. com.). It was not known whether this behavior was critical to successful reproduction in the angonoka and might be affected by the low population densities that exist today. Predation of eggs and young tortoises by the non-native African bush pig was considered one of the primary threats to the survival of the angonoka (Juvik et al. 1981; Curl et al. 1985; Durrell et al. 1989b). Feral pigs are known to destroy nests of birds and reptiles in other parts of the world (MacFarland and Reeder 1975; Coblentz and Baber 1987).

The objectives of this portion of my study were as follows:

1. To identify and describe seasonal activity patterns in the angonoka.
2. To determine whether angonoka were mating and producing young in the Cape Sada population, and if so, to describe mating behavior in the wild.
3. To assess the impact of African bush pigs on angonoka nests.

Methods

Thirteen tortoises (3 males, 5 females, and 5 juveniles with 8-10 shell growth rings) were radio-tagged and followed for periods ranging from 121 to 630 days (see methods in Chapter 3). Tortoises were located by direct observation on seven mornings

(between 0600-1200 hrs) and seven afternoons (between 1400-1800 hrs) per month, weather permitting. Tortoises also were found during monthly visual surveys (Chapter 2). Each time a tortoise was located the date, time, weather (i.e. clear, partly cloudy, cloudy, rain), air temperature, substrate temperature, relative humidity, and behavior were recorded. Minimum and maximum air temperature and rainfall were recorded daily at the Cape Sada camp.

Tortoise behaviors were categorized as resting with the head retracted (R), resting with head out (R/HO), walking (W), feeding (F), courtship (male-female encounters) (CS), combat (male-male interactions)(CO), and nesting (N). Among these behaviors, R was considered inactive, whereas R/HO, W, F, CS, CO and N were considered active. Data were grouped into two seasons for analysis (November – April = wet season; May – October = dry season). Correspondence analysis was used to graphically depict associations among the variables sex, behavior, year, and season (SAS 1992).

In the 1994 nesting season, thread trailers (Breder 1927; Stickel 1950) were used to follow the five radio-tagged females. The trailers consisted of spools of hip-chain replacement thread (Forestry Suppliers, Inc., Jackson, MS) that were encapsulated in 125 ml Nalgene bottles. The bottles were mounted with duct tape on the posterior of the tortoise's carapace, and the end of the thread was tied to a nearby tree or shrub. After 24 hours, the thread trail was searched for evidence of fresh digging that might indicate that the female had nested. The spent thread was collected and measured to determine the

actual distance traveled by the tortoise in a 24-hour period. Nests were left undisturbed but checked periodically for signs of disturbance by predators.

Beginning in February 1995, I radio radio-located females daily in order to observe nesting behavior. Nesting females were observed from a distance until a nest had been completed. Nests were then excavated and eggs were counted. Care was taken not to turn or rotate eggs, and once the eggs had been counted the nest was re-buried. In mid-October, near the end of incubation, chicken wire cages (3-cm mesh) were placed above the nests so that emerging hatchlings could be caught and marked. Cages were anchored with tent stakes and a corner of each cage was shaded with a white cloth to prevent hatchlings from overheating. Cages were checked daily for emerging hatchlings from mid-October onward. Hatchlings were measured (see methods in Chapter 5), marked by painting a unique series of marginal scutes, and released at the nest site.

<div align="center">Results</div>

Seasonal Activity Patterns. Monthly rainfall and air temperatures at the study site are presented in Figure 4-1. More than 70 % of the annual rainfall occurred in January and February for both years of the study, whereas less than 20 mm of rainfall (< 2 % of total) was recorded during the dry season. During the wet season (November – April), the mean minimum temperature was 24.2 °C as compared to 20.5 °C in the dry season (May – October). In the wet season, the average maximum temperature was 34.0 °C, whereas in dry season the average maximum was 32.8 °C

In most observations, radio-instrumented angonoka were inactive, resting with their head-in (R/HI) under vegetation (Figure 4-2, 4-3, and 4-4). When behaviors were categorized as either "inactive" or "active", seasonal differences in activity levels were evident (Figure 4-5). These differences were statistically significant for all sex/life stages (Table 4-1). Tortoises often stopped walking or feeding when they were approached. While this probably resulted in an under-representation of feeding and walking observations, tortoises rarely retracted their head when disturbed, and were still categorized as resting-head-out, an "active" behavior.

Active tortoises were observed throughout the day (0600 hrs – 1700 hrs); however, observations were most frequent from 1100 hrs to 1200 hrs (Figure 4-6). No nocturnal activity was observed in this study. Tortoises were active at a wide range of air temperatures (22-45°C) and substrate temperatures (21-44°C). Tortoises were active when the relative humidity was 33-98%.

Results of the correspondence analysis revealed that variables such as walking and resting/head-out (active behaviors) were closely associated with the wet season, whereas, resting head-in (inactive) was more closely associated with the dry season. Correspondence analysis represents each season, year, sex/life stage, and behavior on a plot (Figure 4-7), where the relative positions of the points indicate similarities and differences. On the plot, the cosine of the angle between two points indicates the affinity of those two categories for one another. A large, cosine (small angle) indicates high affinity.

In addition to observations of the behavior of radio-instrumented tortoises, tortoises were incidentally encountered during the course of timed visual surveys and other field tasks (322 observations). Most of the tortoises encountered during visual surveys were active. Despite the experience of surveyors, tortoises were very difficult to find when they were inactive and resting under vegetation. Overall, incidental observations of tortoises reflected activity patterns similar to those of radio-instrumented tortoises. Most observations occurred during the wet season (76 %) when tortoises were most often out walking, feeding, mating, or nesting.

Mating Behavior. Male angonoka were most active from November through January, which corresponded roughly with the reproductive season (Figure 4-2). Courtship was observed on 8 occasions over the two-year period. All observations occurred in November and December (Table 4-2). Male-male interactions consisted of one male circling, ramming, and chasing the other tortoise, followed by the retreat of one of the males. Male-male interactions lasted from 5 to 25 minutes. Male-female encounters were observed five times and observations ranged from 35 to 58 minutes in length. The general pattern of behaviors recorded between male and female tortoises included the male pursuing the female, bumping the rear of the carapace with the gular, and circling the female repeatedly before mounting her. On two occasions the male tortoise actually overturned the female using the gular. One of the overturned females was able to right herself, whereas the male righted the other as he continued ramming her with his gular. During copulation, males emitted a wheezing vocalization. The smallest

male and female observed mating were 398 and 338 mm CL, respectively. The largest

male marked in the Cape Sada population and the largest female were observed mating.

Nesting Behavior. Female angonoka nested from February through May and one

female attempted to nest in June (Table 4-3). In October 1993, a nest containing 5 eggs

was found during visual surveys. The nest was very shallow and one egg was visible at

the soil surface. Three nests were located using thread trailers during the 1994 nesting

season. Nests were well hidden and difficult to locate unless the tortoise had buried part

of the thread in the egg chamber. By increasing the frequency of radio-location during

the 1995 nesting season, 8 nests were discovered. On two occasions females produced

multiple clutches within a single season. The maximum number of clutches per season

was three. The internesting interval ranged from 22 to 30 days (n=4).

Tortoises often attempted to nest for several days before successfully depositing

eggs. During a typical failed nest attempt, the female excavated an egg chamber but

abandoned it when she encountered obstructions in the soil such as rocks or roots. One

female attempted to nest on 11 occasions over a 10 day period before depositing eggs

(See Table 4-3).

Most nesting activity occurred in scrub-shrub microhabitat (71.7 %) followed by

bamboo (23.9 %), open (2.2 %) and grass habitat (2.2 %). Females nested in the four

microhabitats relative to their availability ($\chi^2 = 9.57$, df= 4, $P > 0.05$). They typically

nested at the base of a shrub or bamboo plant; however, one nest was constructed in an

open sandy area with no vegetation. Another nest was deposited in an area within the scrub-shrub microhabitat that had been heavily disturbed by pigs.

Peak nesting activity occurred in April through June in 1994, and in March and April in 1995 (Figure 4-8). Nesting activity was recorded from 0736-1645 hrs, but most activity took place in the morning between 0800 and 1100 hrs (Figure 4-9). The thread trailer method provided information on the length of nesting forays of individual females. The mean distance traveled by females in the 24-hour period before nesting was 195.08 m (n= 12; range = 25.0 – 626.5) as compared to only 31.71 m in the 24-hour period following nesting (n= 5; range = 0.0 – 57.3). The maximum distance traveled by a female on a nesting foray was 626.5 m in a 12-hour period.

Clutch size for the 12 nests ranged from 2-5 eggs with a mean of 3.36±0.92 (Table 4-3). The smallest female known to have nested was 345 mm CL. Clutch size varied positively with carapace length, although the relationship was not statistically significant (F= 3.17; df= 10; P= 0.11). Incubation ranged from 220 to 244 days and hatchlings emerged between 5 November and 18 December. A hatchling was discovered within a nest in late October 1994, suggesting that angonoka may exhibit delayed emergence from the nest. Hatchling emergence appeared to coincide with the onset of seasonal rains and if undisturbed, this hatchling may have remained in the nest chamber. Forty-one percent of all eggs hatched successfully (Table 4-3), but hatching success varied a great deal among nests. Only one nest had 100 % hatching success and 4 of the 12 nests (33 %) produced no hatchlings. The overall hatching success at the captive

breeding center was 42 % and hatching success among individual nests was quite variable (Reid 1995). No nest predation was observed in this study. However, one nest was destroyed by African bush pigs following this study (M. Pedrono, pers. com.).

Hatchling and Juvenile Behavior. Twenty hatchling angonoka were observed walking and feeding from January through April (Figure 4-10). Incidental observations of active small juvenile tortoises (<85 mm CL) peaked in February through March. Hatchlings and small juveniles were most often observed walking or feeding in the open microhabitat (80% of observations) between 0735 and 1727 hrs.

Feeding Behavior. Tortoises were observed feeding on 78 occasions (2.5 % of all observations). All feeding behavior was observed from October through May, with most observations (n= 15) occurring in April. Adults were observed feeding in the open microhabitat more often than would be expected based on habitat availability (χ^2= 102.91, df= 4, P< 0.0001) (Figure 4-11). They consumed small herbs and forbs typical of these areas. Juveniles fed in the bamboo microhabitat more often than expected. Although food plants were not identified to species in this study, in most observations (44 %), tortoises fed upon herbs, forbs and shrubs (*Bauhinia* spp. and *Terminalia* spp.) rather than grasses (15.6 %). Tortoises were never observed feeding on live bamboo; however, on several occasions they consumed leaf litter that included dead bamboo leaves (15.6 %). Angonoka were observed feeding on dried carnivore feces (12.5 % of observations) and African bush pig droppings (12.5 %). Of the three life stages, juveniles most often were observed consuming feces (87 % of observations).

Discussion

As expected, given the highly seasonal environment in the Baly Bay region, angonoka exhibited seasonal differences in activity patterns. Tortoises were significantly more active during the wet season than during the dry season. Seasonal differences in activity patterns also were evident in tortoises observed during visual surveys (see Chapter 2). These results suggest that whenever possible, tortoise surveys should be concentrated in December, January and February. Activities such as mating and nesting occurred only in wet season months (Figure 4-12). Hatchlings emerged with the onset of seasonal rains. Small juveniles were active and highly visible from February through March. These tortoises were undoubtedly vulnerable to diurnal predators at this time. The primary diurnal predators in the region are the Madagascar buzzard and yellow-billed kite.

Although mating was observed on only a few occasions, the behavior patterns were similar to those described for captive angonoka and radiated tortoises (*Geochelone radiata*) (Auffenberg 1978; McKeown et al. 1982; Reid 1989). Male angonoka exhibited considerable agonistic behavior in competition for females. In addition, males made long forays in the early wet season, presumably in search of mates (Chapter 3). Further description of the mating system of the angonoka is needed. Home ranges of adult males and females overlapped considerably during the wet season (Chapter 3). However, the ranges of adult males overlapped very little. It will be important to examine the degree of

overlap among all males in the population in order to determine if male angonoka exhibit a dominance hierarchy (Harless 1979).

The smallest reproductively active male and female observed in this study were 398 and 329 mm CL, respectively. However, it is likely that angonoka are sexually mature at a smaller size than was detected based solely on observations of mating. Secondary sexual characteristics could generally be distinguished in tortoises that were greater than 300 mm CL or with greater than 15 shell growth rings (Chapter 5). Demographic variables such as size (and age) at first reproduction in the angonoka should be determined in the future.

The maximum number of clutches produced by a female in a single season was three, which was considerably less than that recorded in captive angonoka. At the breeding center in Madagascar, females nested up to 7 times in a season and the nesting period extended from January through July (Reid 1995). This difference could be an artifact of the field sampling methodology, because it is likely that some nesting activity of radio-instrumented females was not detected. However, captive females receive a different diet than wild tortoises, and are given supplemental calcium during nesting season (Reid 1995). Differences in the nutritional status between wild and captive tortoises could explain the apparent difference in reproductive output.

Reproductive output in chelonians is a product of clutch size and frequency and egg size. Two general reproductive patterns have been described for aquatic or semi-terrestrial chelonians (Moll 1979). The first pattern, typical of sea turtles, is that of

producing multiple clutches of many small eggs in a discreet nesting season. The second pattern, typified in tropical mud turtles and box turtles, consists of small clutches of large eggs with acyclic or continuous nesting. In testudinids, larger species (e.g., *Geochelone*) tend to lay larger clutches, whereas smaller species tend to be more specialized, and often produce very small clutches. The angonoka is a large species that produces small clutches and appears to be an exception to this pattern. The largest reported clutch size in the angonoka was 6 eggs (Pedrono 1997; Reid 1995) and the mean clutch size in this study was 3.2±0.92 eggs. In contrast, *G. radiata* produces much larger clutches with 3-12 eggs (Zovickian 1973). It will be important to examine reproductive output in wild angonoka more closely in the future, and to look for differences among the 5 populations.

Incubation length in this study (220 days) was similar to that reported for nests of captive angonoka (215 days)(Reid 1995). No information on incubation of wild radiated tortoises is available, however, in the average incubation period for captives of this species ranged from 155-230 days depending on incubation temperature (Zovickian 1973; Burchfield 1975).

Although hatching success of the wild nests in this study (41 %) was similar to that reported for in-situ nests at the captive breeding center (42 %) (Reid 1995), it was low compared to other species of tortoise (Landers et al. 1980; Smith 1995). It is not known whether the unhatched eggs were infertile or failed to hatch because of a developmental problem. Eggs seldom were removed from the nest as they were counted, and when it was necessary to handle the eggs, care was taken not to turn or roll them.

Therefore I feel it is unlikely that handling had an effect on hatching success in this study.

If female angonoka produce 3.36 eggs per clutch and three clutches per year (a conservative estimate based on this study and captive angonoka), the 27 adult female angonoka on Cape Sada would be expected to produce a total of 272.2 eggs per year. This calculation is based on the unproven assumption that all females nest annually. If the 41 % hatching success observed in this study is typical for this species, then the adult population of angonoka on Sada would be expected to produce 112 offspring per year. Although nest predation was not observed in this study, the predation rate on small juveniles may be high (see Chapter 2). High mortality in the early life stages of terrestrial turtles is not uncommon (Ehrenfeld 1979; Diemer 1986). Long-term data are needed to evaluate survivorship of juvenile angonoka in order to determine whether recruitment to adulthood is occurring in this population. In a relatively stable environment (particularly with no removal of adults from the population), a long-lived species such as the angonoka may be capable of recovering from past exploitation without augmentation with captive born juveniles. However, loss of breeding adults could have catastrophic consequences.

Although the number of nests monitored in this study was limited, the lack of nest predation was somewhat unexpected. High nest predation rates have been reported in other chelonians (Wilhoft et al. 1979; Landers et al. 1980; Siegel 1980; Congdon et al. 1987; Hailey and Loumbourdis 1990). Despite a great deal of bush pig activity on Cape

Sada, many tortoise nests clearly are surviving to produce hatchlings. Information is needed regarding nest predation at other angonoka populations. I suspect that pigs may exert a more subtle effect on the angonoka by altering the habitat and soils. Bush pig rooting was extensive on Cape Sada throughout the course of this study. Cattle also are present on Cape Sada and may be altering the habitat and soil structure. In heavily grazed areas in Argentina, cattle compact the soil above tortoise nests and injure young tortoises (Waller and Micucci 1997). The potential impacts of bush pigs and cattle on the angonoka should be investigated. Cattle are an important part of the Sakalava culture (Durbin et al. 1996) and it will be difficult to resolve problems involving interactions between cattle and tortoises. If bush pigs are proven to negatively impact tortoises, control of this species will present a different problem. Local people are reluctant to handle bush pigs for religious reasons. If necessary, it may be possible to hire outside contractors to remove pigs.

Table 4-1. Percent of observations where tortoises were active (walking, feeding, combat, courtship, or nesting). * indicates $P < 0.0001$.

% Active Observations

Sex/Life Stage	Wet Season	Dry Season	Chi-square Value
Males	82.3	17.7	82.75*
Females	77.3	22.7	127.44*
Juveniles	83.2	16.8	102.22*
All Tortoises	80.0	20.0	309.48*

Table 4-2. Information on breeding behavior in the angonoka (*Geochelone yniphora*) on Cape Sada. Data were collected from October 1993 through June 1995. *nd= no data.

TYPE OF INTERACTION	DATE	TIME	DURATION OF OBSERVATION (IN MINUTES)*	TORTOISE ID/ CARAPACE LENGTH (IN MM)
Male-Male	11/17/93	0825	5.18	47 (402)
				52 (406)
	12/28/93	1610	<5	57 (431)
				58 (438)
	11/28/94	0827	30	54 (454)
				59 (456)
Male-Female	11/23/93	0700	58	47 (402)
				9 (344)
	12/16/93	0830	57	54 (454)
				55 (338)
	12/20/93	0824	nd	13 (398)
				12 (361)
	11/4/94	0755	35	52 (406)
				12 (361)
	11/22/94	0913	nd	59 (456)
				43 (405)

Table 4-3. Nesting activity in the angonoka (*Geochelone yniphora*) during the 1994 and 1995 nesting season at Cape Sada, Madagascar.

YEAR	DATE	TIME	HABITAT	TORTOISE ID	DESCRIPTION
1994	Feb 22	0742	SS	3	Attempt only
	Mar 2	0938	BA	3	Attempt only
	Mar 4	0736	SS	6	Attempt only
	Apr 8	AM	SS	12	Attempt only
	Apr 9	AM	SS	12	4 eggs
	Apr 25	0855	BA	19	Attempt only
	Apr 25	1540	BA	19	3 eggs
	Apr 26-30	ND	SS	9	Several attempts
	May 12	0829	SS	12	Attempt only
	May 12	0937	SS	1	Attempt only
	May 13	0908	OP	1	3 eggs
	Jun 7	0911	BA	9	Attempt only
	Jun 15-25	ND	SS	9	11 attempts
1995	Feb 24	1005	BA	19	4 eggs
	Mar 18	1200	SS	19	4 eggs
	Mar 20	0921	BA	12	3 eggs
	Apr 13	0859	SS	19	4 eggs
	Apr 19	0845	BA	12	2 eggs

Table 4-4. Angonoka (*Geochelone yniphora*) nest data for the 1994 and 1995 nesting seasons on Cape Sada, in western Madagascar.

IDNO	DATE	HATCHING DATE	INCUBATION LENGTH (DAYS)	CLUTCH SIZE	HATCHING SUCCESS	HABITAT
00	nd	12/11/94	Unknown	5	40%	SS
12	4/9/94	10/26/94; 12/9/94	220; 244	4	50%	SS
19	4/25/94	12/16/94; 12/18/94	235; 237	3	67%	BA
1	5/13/94	_____	_____	3	0%	OP
19	2/24/95	11/13/95; 11/19/95	264; 270	4	50%	BA
19	3/18/95	11/5/95	232	4	50%	SS
12	3/20/95	_____	_____	3	0%	BA
8	3/24/95	11/15/95	236	2	50%	SS
1	3/25/95	12/18/95	268	2	50%	BA
19	4/13/95	12/3/95	234	4	100%	SS
12	4/19/95	_____	_____	2	0%	BA
3	3/27/95	_____	_____	3	0%	BA
			Total:	39	41.02 %	
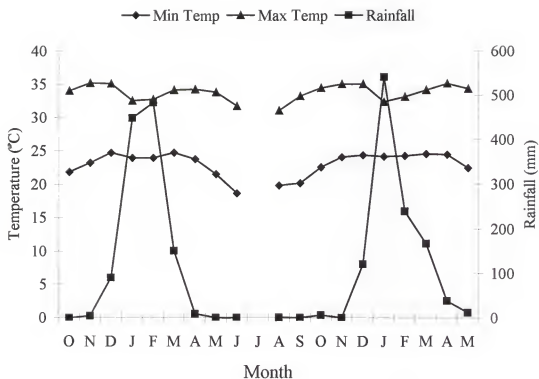
Figure 4-1. Monthly rainfall and temperature data collected at Cape Sada in western Madagascar, form October 1993 through May 1995.
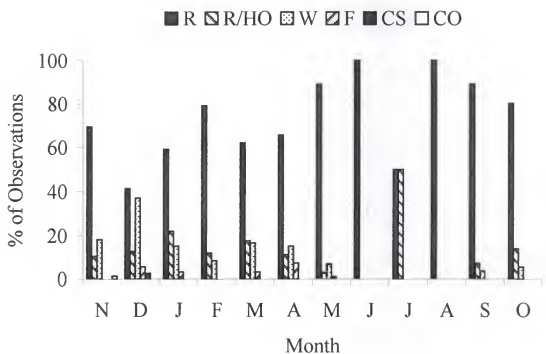
Figure 4-2. Monthly behavior patterns for three radio-instrumented adult male angonoka (*Geochelone yniphora*) on Cape Sada, Madagascar. R= resting head-in; R/HO= resting head-out; W= walking; F= feeding; CS= courtship; and CO= male-male combat.
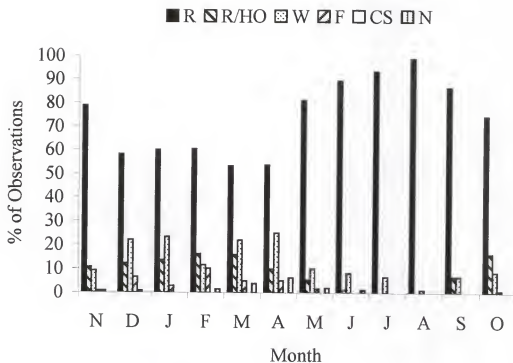
Figure 4-3. Monthly behavior patterns for five radio-instrumented adult female angonoka (*Geochelone yniphora*) on Cape Sada, Madagascar. R= resting head-in; R/HO= resting head-out; W= walking; F= feeding; CS= courtship; and N= nesting.
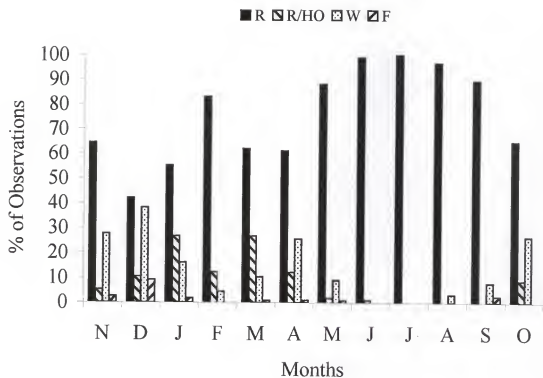
Figure 4-4. Monthly behavior patterns for five radio-instrumented juvenile angonoka (*Geochelone yniphora*) on Cape Sada, Madagascar. R= resting head-in; R/HO= resting head-out; W= walking; F= feeding.
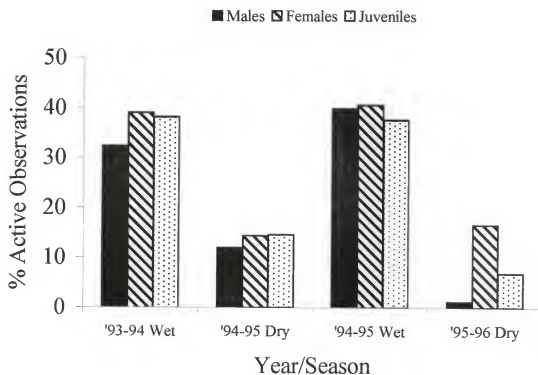
Figure 4-5. Seasonal activity patterns of 13 radio-instrumented angonoka (*Geochelone yniphora*) on Cape Sada, Madagascar. Wet season extended from November through April and dry season from May through October.
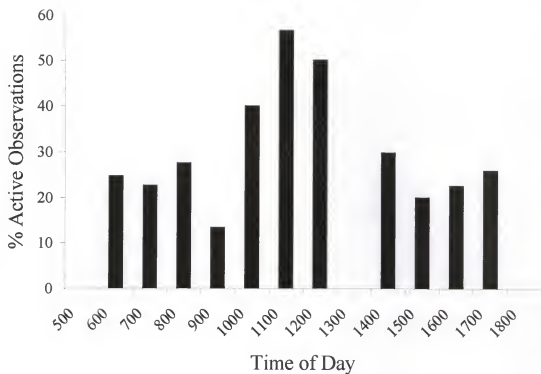
Figure 4-6. Percent of observations of active angonoka (*Geochelone yniphora*) by time of day on Cape Sada, Madagascar.
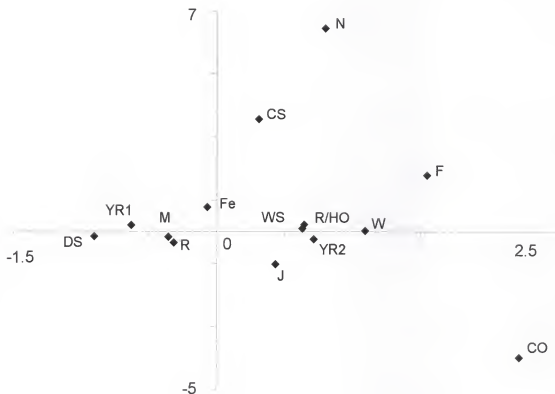
Figure 4-7. Results of correspondence analysis depicting the relationship among behavior, season, sex/life stage, and year in angonoka (*Geochelone yniphora*). R= resting head-in; R/HO= resting head-out; W= walking; F= feeding; CS= courtship; and N= nesting; WS= wet season; DS= dry season; M= male, Fe= female, J= juvenile.
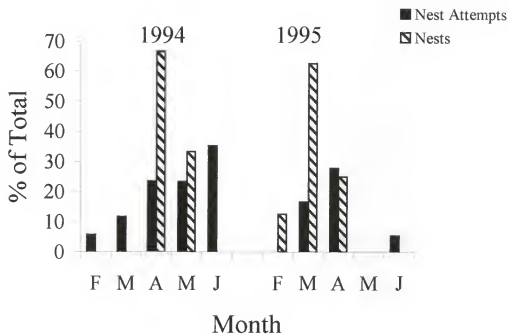
Figure 4-8. Nesting activity by month in the angonoka (*Geochelone yniphora*) on Cape Sada, Madagascar.
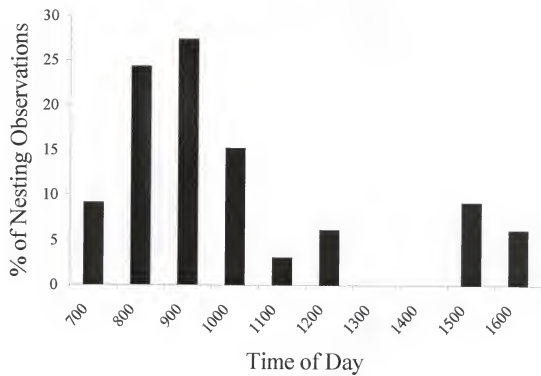
Figure 4-9. Nesting activity by time of day in the angonoka (*Geochelone yniphora*) on Cape Sada, Madagascar.
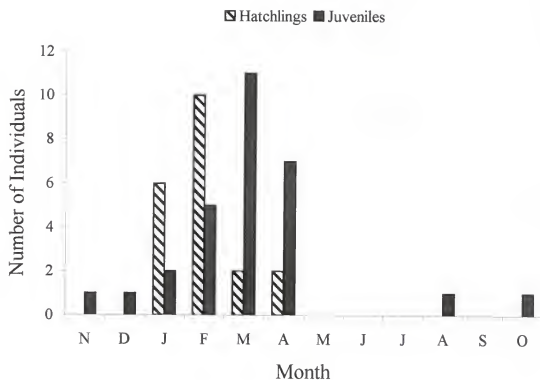
Figure 4-10. Monthly observations of hatchling and juvenile angonoka (*Geochelone yniphora*) on Cape Sada, Madagascar.
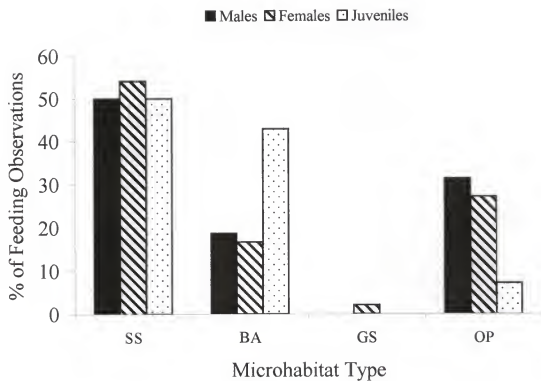
Figure 4-11. Feeding observations by microhabitat type for angonoka (*Geochelone yniphora*) on Cape Sada, Madagascar. SS= scrub-shrub; BA= bamboo; GS= grasses; OP= open.
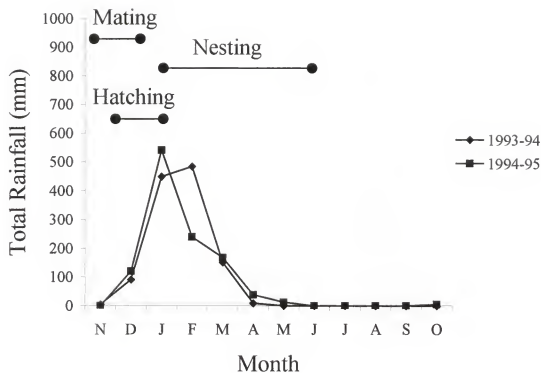
Figure 4-12. Behaviors of the angonoka (*Geochelone yniphora*) as related to rainfall on Cape Sada, Madagascar.

CHAPTER 5
MORPHOLOGY

Introduction

Early descriptions of *Geochelone yniphora* were based on very few specimens
(Vaillant 1885; Vaillant 1889; Siebenrock 1903; Angel 1931). Although later reports
were more comprehensive (Juvik et al. 1981), small sample sizes still precluded a
detailed description of the species. Similarities between *G. yniphora* and the closely
related radiated tortoise (*G. radiata*) were noted. However, the angonoka is the larger of
the two species, is somewhat less colorful, and has an elongate, undivided gular
projection. The angonoka received its English common name, the ploughshare tortoise,
from the long, recurved gular.

Based on early descriptions, adult angonoka appeared to exhibit sexual
dimorphism. This phenomenon is well documented in the general literature (Carr 1952;
Graham 1979; Pritchard 1979; Ernst and Barbour 1989). Divergent characters such as
body size, shell morphology, and tail size, often are used in determining the sex of turtles.
The posterior portion of the plastron in males of some species is concave, which aids in
stabilizing the male as he mounts a female prior to copulation. This phenomenon is most
pronounced in highly domed, terrestrial species such as the red-footed tortoise
(*Geochelone carbonaria*), yellow-footed tortoise (*Geochelone denticulata*), radiated

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tortoise (*Geochelone radiata)*, and box turtle (*Terrapene carolina*) (Nichols 1939; Legler 1963; Pritchard 1979; Dodd 1997). Adult males of several tortoise species have an elongated gular projection. Gopher tortoises (*Gopherus* spp.) and angulated tortoises (*Chersina angulata*), among others, use the long gular as a battering ram in courtship rituals (Auffenberg 1966; Douglass 1976; Boycott and Bourquin 1988).

McRae et al. (1981) noted a difference in alignment of the xiphiplastra and pygal bones of male and female gopher tortoises. The anal notch measurement was significantly larger in females than in males and males had a greater anal width. Presumably, the large anal notch in females allows passage of large diameter eggs. The size of the hind opening is probably the result of a trade-off between vulnerability to predation and egg size. The wide anal fork in males apparently allows lateral movement of the tail prior to copulation.

In addition to differences in shell morphology, in most Testudines, males have longer, thicker tails and a more distally located vent than females. This occurs because, in a relaxed state, the penis is completely contained within the cloaca. This character is consistent across a wide array of taxa (Carr 1952; Pritchard 1979; Ernst and Barbour 1989).

In many adult turtles, the sexes are markedly different in size. The most extreme example of sexual size dimorphism (SSD) occurs in the Brahminy River turtle (*Hardella thurji*), a poorly known species from India and Pakistan. Adult male *H. thurji* attain a carapace length of only 18-20 cm as compared to 53-65 cm in females (Minton 1966;

Tikader and Sharma 1985). Members of the genus *Graptemys* also show marked size dimorphism. For example, female Barbour's map turtles (*Graptemys barbouri*) may attain a carapace length of 27 cm, which is more than twice that of males (Carr and Marchand 1942). Size variation is less dramatic in species in which males are larger than females. For example, in Galapagos tortoises (*Geochelone nigra*), males may attain a length of 150 cm as compared to 110 cm in females (MacFarland et al. 1974).

In most size dimorphic species, females attain greater body size than males, but there are a number of species in which males are larger than females. The selective advantages of large or small relative body size between the sexes are not fully understood. Possible explanations for the evolution and maintenance of SSD include selection for characters that enhance the access of one sex to the other (Berry and Shine 1980). For example, selection for large size in males might be expected if there is a high degree of intraspecific competition for females. In *Geochelone sulcata*, *Dipsochelys dussumieri*, and *C. angulata*, males are larger than females and all have combat rituals for access to females (Pritchard 1979; Ernst and Barbour 1989). However, male *Geochelone elegans*, *G. denticulata* and *G. polyphemus* are smaller than females and also display agonistic behavior (Ernst and Barbour 1989). It also has been suggested that the occurrence of SSD in turtles is related to habitat. In slow, bottom walking aquatic species where "forced insemination" occurs (e.g., most Kinosternids), males are larger than females (Berry and Shine 1980). In contrast, in fast swimming aquatic species (e.g., most emydids), where females could easily escape a male, female choice is the breeding

mechanism. Therefore, in this case, selection has favored evolution of an elaborate courtship display over body size.

Pritchard (1979) made the general statement that among large turtles [e.g., giant tortoises (*Geochelone nigra*) and African spurred tortoises (*G. sulcata*)], males are larger than females, whereas in the smaller species (e.g., *Trachemys* spp. and *Pseudemys* spp.), females are larger than males. He argued that, in comparatively small species, it is advantageous for females to be large so they can accommodate a larger clutch size. Maternal body size in turtles often is correlated with clutch size, which is a measure of reproductive effort (Congdon and Gibbons 1985; Mitchell and Pague 1990). In contrast, in giant tortoises, where egg volume is small relative to female body size, there is no advantage in females being larger than males. There are exceptions to this generalization, including *Podocnemis expansa*, a large aquatic species, in which females are much larger than males. In contrast, the angulated tortoise (*C. angulata*) is a relatively small species (ca. 27 cm carapace length) and males are larger than females.

Secondary sexual characteristics can be very useful in distinguishing sex in adult turtles; however, the subjective use of such characters may result in misidentification. Although early reports suggested that angonoka were sexually dimorphic, accurate morphological measurements of free ranging tortoises were needed as verification. Therefore, the first objective of this portion of the study was to quantify differences in shell morphology between adults of both sexes, and to determine which morphological characters could best be used to distinguish between the sexes. The determination of age

at first reproduction is one of the most important demographic variables in turtle populations (Auffenberg and Iverson 1979). Therefore, a second objective of this study was to attempt to determine the size/age at which secondary sexual characteristics could be distinguished in the angonoka. This might provide an estimate of age at first reproduction. The third objective was to provide a general physical description of the species to supplement earlier reports that were based on examination of very few individuals.

Methods

A total of 143 angonoka were examined from 1993 through 1995. Tortoises were located during visual surveys (Chapter 2) at five localities in the Baly Bay region. Localities include Cape Sada (97 tortoises), West Baly Bay (25), Beheta (18), Ankasakabe (2), and Betainalika (1). At time of first capture, all tortoises were marked and a series of shell measurements were taken. Adult and subadult tortoises were permanently marked by notching a unique series of marginal scutes. The marginal scutes of hatchling and small juvenile tortoises were marked with enamel paint. Shell measurements taken included straight-line carapace length (CL), shell height (HT), carapace width (CW), plastron length (PL), gular length (GUL), anal notch (AN), and anal fork (AF) (Figure 5-1). CL, PL, HT, and CW of tortoises with greater than 100 mm carapace length were measured to the nearest 1.0 mm using Haglof Mantax aluminum calipers (Forestry Suppliers, Inc. Jackson, MS). A metric dial caliper (accurate to the

nearest 0.01 mm) was used to measure GUL, AF, and AN of adult tortoises and CL of hatchling and juveniles less than 100 mm in length. Wet body mass of adult and subadult tortoises was taken with a 20-kg Pesola spring scale (accurate to the nearest 100-g) and juveniles were weighed with a 300-g Pesola scale (accurate to the nearest 10-g). Radio-instrumented tortoises were re-measured and weighed at 6-month intervals from August 1993 through June 1995.

In a strongly seasonal environment, some chelonians deposit a single scute growth layer annually, and counting the number of layers or rings is a reasonable method of estimating age (Cagle 1946; Sexton 1959; Gibbons 1970; Galbraith and Brooks 1987). However, whenever possible, this method of age estimation should be tested with known age individuals (Woodbury and Hardy 1948; Dobie 1971; Zug 1991). Growth rings were generally easy to distinguish in angonoka, and because of the distinctly seasonal environment in the region, they may well provide an accurate estimate of age. Therefore, for analyses in this study, scute growth rings were used as an estimate of age. Rings were counted using the first or second costal plate following methods outlined in Zug (1991). When all rings could not be distinguished, an estimate of the minimum number of rings was made. Scutes were counted and any anomalies were recorded. Where possible, tortoises were photographed from a dorsal, ventral, and lateral view.

The sex of adult tortoises was determined based on general differences in shell morphology (gular length, plastral concavity, and anal notch/anal fork ratio) and tail size. Ideally, such distinctions should be confirmed with an examination of reproductive

organs (e.g., McRae et al. 1981); however, this was not possible in my study. Therefore, wherever possible, sex of adult tortoises was confirmed with behavioral observations.

Logistic regression (SAS 1992) was used to build a model for determining which shell characteristics were most significantly related to gender in the angonoka, and for predicting gender of adults angonoka based on these measurements. The explanatory (predictor) variables in the model consisted of a subset of shell characteristics measured in the field. The characters used in the model were chosen using forward selection.

The degree of sexual size dimorphism (SSD) was quantified using the compressed Sexual Dimorphism Index (SDI- Lovich and Gibbons 1992).

$$SDI = \frac{\text{size of larger sex}}{\text{size of smaller sex}} + 1.$$

The SDI is arbitrarily defined as negative if males are larger than females, and positive if females are larger than males. This index was developed to allow direct comparison of the degree of SSD across taxa.

Results

General Description. Shell color of the angonoka examined was dull yellow or tan with dark brown or black margins on the vertebral and costal scutes. The marginal scutes were transected by a dark triangular pattern that extended from the ventral portion of the scute downward. Dark triangles also appeared on the plastron and radiated from

the midline through the pectoral, abdominal, and femoral scutes. The shell pattern was much less distinct, or entirely absent in large individuals. Old/large tortoises tended to be uniformly dull yellow or tan in color. Hatchlings also had dark margins on the vertebral and costal scutes, but the marginal scutes lack the dark triangles visible in larger individuals. The skin of angonoka of all ages was tan, although the heads of some adults was dark brown or nearly black.

All tortoises examined had an extremely high shell profile. The ratio of mean HT to mean CL (shell domedness) was 0.617 (n= 143; range= 0.495-1.014, SD= 0.057). The rear marginals of large adults were flared. As described by Ernst and Barbour (1989), the angonoka examined in this study angonoka typically possessed a cervical (nuchal) scute, 5 vertebrals, 8 costals, 22 marginals. The supracaudal usually was undivided. Three individuals (2 % of sample) lacked a cervical scute. Three tortoises, two adult females and one adult male, lacked a gular entirely. The number of marginal scutes typically was 22; however, two individuals had only 21 and a third tortoise had 23 marginals.

Descriptive statistics for morphological measurements taken are presented in Table 1. The largest angonoka was a male with 481 mm CL. Sixteen of the 72 juveniles were newly emerged hatchlings with a mean CL of 47.2 mm (range= 43.5 – 52.0, SD= 3.0). Free ranging hatchlings were comparable in size to captive born offspring (Reid 1987, 1988).

Growth. Growth data were collected for 20 tortoises in the Cape Sada population. Little change in CL was detected in adult tortoises (Figure 5-2). This was not

unexpected, given the short length of the study and the fact that growth in turtles slows markedly after maturity (Ernst and Barbour 1989; Wilbur 1975). In contrast, juvenile angonoka exhibited substantial growth. On average, CL of the five juveniles (156-173 mm-initial CL) monitored in this study increased 19.51 mm per year. Most tortoises showed an overall increase in body mass from October 1993 through May 1995; however, body mass typically fluctuated with season (Figure 5-3). There was variation in this pattern among individuals, which might be explained by females carrying eggs or nesting prior to weighing in the wet season.

The number of shell growth rings was linearly associated with CL (Figure 5-4, $r^2 = 0.94$); however, in large tortoises the relationship was not as strong. This is consistent with an attenuated growth pattern. Growth in turtles generally slows once an individual attains sexual maturity. The maximum number of shell rings that could be counted was 33, and while rings could be easily distinguished in most individuals, the shells of large tortoises tended to be worn smooth. The five juvenile angonoka monitored at 6-month intervals over the course of the study accrued one growth ring per year.

Sexual Dimorphism. The smallest male that exhibited obvious secondary sexual characteristics was 262 mm CL, whereas the smallest female was 280 mm CL. However, in general, secondary sexual characteristics could be distinguished in tortoises greater than 300 mm in CL or with approximately 13-16 scute growth layers. Therefore, I suspect that angonoka obtain sexual maturity at approximately 15 years of age.

The mean CL of adult male angonoka was significantly greater than that of adult females (t= 3.53; df= 54; P= 0.0009); however, no difference in wet body mass between the sexes was detected (t= -1.58; df= 59; P= 0.12). Body mass probably is not a good character for evaluating sexual dimorphism in the angonoka because it tended to fluctuate seasonally. The SDI, using CL as a measure of body size, is -1.10.

Results of logistic regression analysis for the individual shell characters GR, CL, CW, HT, PL, GUL, AN, and AF of adult angonoka are presented in Table 5-2. Of these characters, CL, PL, GUL, AN, and AF were significantly different among the sexes. Differences between CW and HT approached significance. The characters CL and PL, CL and CW, and PL and GUL were highly correlated (Pearson Correlation Coefficients = 0.90, 0.93 and 0.89, respectively). Therefore, these combinations of characters were not used in the logistic regression model. The logistic regression model used the characters GUL, AN, and AF. Type III likelihood ratio statistics for these three shell characters are presented in Table 5-3.

The equation for the logistic regression model is:

$$\pi = \frac{e^{\,4.2335+(0.1926 \times AF) - (0.9852 \times AN) + (0.4663 \times GUL)}}{1 + e^{\,4.2335+(0.1926 \times AF) - (0.9852 \times AN) + (0.4663 \times GUL)}}$$

Pi (π) represents the probability that the tortoise is a male. In other words, in adult angonoka, if π is close to one, the animal is likely to be a male, whereas, if it is close to zero, the animal is likely to be a female.

Of those characters originally considered sexually dimorphic in the angonoka, the difference in AF was most distinct. All tortoises with an AF greater than 75.5 mm were male (Figure 5-5). Gular length also was a good predictor of sex in adult tortoises; however, several females had surprisingly long gular projections (Figure 5-6). Differences in AN also were apparent in adult angonoka (Figure 5-7). Although early descriptions suggested that the carapace of female angonoka was more domed than that of males, no statistically significant difference in "domedness" (the ratio of mean HT/CL) was detected between the sexes (t= 1.72; df= 69; P= 0.09).

Discussion

The three morphological characters that appeared to best predict sex in adult angonoka were AF, AN, and GUL. The differences observed probably are directly related to reproduction. For example, the configuration of the xiphiplastron (AF) and supracaudal bones (AN) of the female angonoka probably accommodates the largest possible egg. The size of the opening at the rear of the shell probably is a trade off between allowing the passage of the largest possible egg and affording protection against predators (McRae et al. 1981). Male *G. radiata* also have an anal fork that is broader than the anal notch (Auffenberg 1978). It has been suggested that the wide AF in males of some species allows the male to move the tail freely during copulation (McRae et al. 1981).

The long gular of adult male angonoka also has functional significance in reproduction. Males used the gular to ram other male tortoises when in combat for females (Chapter 4). During courtship, males also used the gular to corral females; they tended to circle the female repeatedly while ramming her with the gular as she attempted to walk away. Interestingly, in several adult females gular length was comparable to, or greater than, that of some males. It is difficult to imagine the function of the long, recurved gular in female angonoka. Juvik and Blanc (1974) mentioned that local people believed that angonoka used the gular like a plow when looking for food. They disregarded this account, and indeed, in this study, angonoka were never observed using the gular in this manner. It has been reported that local people believe the long gular of male angonoka prevents the animal from eating, thus explaining the rarity of the species (Juvik and Blanc 1974; Curl et al. 1984). I found no evidence that the gular of male angonoka impeded normal behavior of angonoka in any way.

Although shell height and domedness did not differ significantly between the sexes in the angonoka, a generally more elongate body shape has been noted in *G. radiata* (Auffenberg 1978), *G. sulcata* (Lambert 1993), and *G. pardalis* (Lambert 1995). Although plastral concavity was not measured in this study, all adult male angonoka had a distinctly concave plastron. Several large females also had a slightly concave plastron. It would be worthwhile to quantify differences in this feature in male and female angonoka in the future and, if significant differences are found, it might be useful to include it in the logistic regression model. McRae et al. (1981) found that plastral

concavity was the most reliable secondary sexual characteristic for differentiating between male and female gopher tortoises. However, old females of this species developed a markedly concave plastron as well. A second character not measured in this study, thickness of the xiphiplastron, also may be useful in distinguishing between the sexes of angonoka. Auffenberg (1978) noted that male *Geochelone radiata* have a thicker xiphiplastron than females.

Adult male angonoka in this study were significantly larger than females. On average, adult male angonoka were 9.8 % larger than females. This is similar to that reported for *G. radiata*, where males are 7.3 % larger than females (Auffenberg 1978). The SDI for angonoka was −1.10. This is consistent with Gibbons and Lovich's (1990) prediction of a relationship between SDI and shell domedness. In the species they examined, the most highly domed species males typically were the same size or larger than females (resulting in a negative SDI). This pattern of sexual size dimorphism also has been observed in the Florida box turtle, another highly domed species (Dodd 1997). Dodd (1997) suggested that larger size in male Florida box turtles probably had a simple mechanical function in allowing males to more easily mount the highly domed females. This explanation also could apply to the angonoka. In addition, selection may favor large size in male angonoka because of the high degree of intraspecific competition for females. The size discrepancy also may allow the male to overpower the female and mate successfully.

Additional data are needed on growth rates in the angonoka and on the relationship between growth rings and age in this species. While use of growth rings in estimating age has proven valid for a number of chelonian species (Germano and Bury 1998), its use has been questioned in others (Cox et al. 1991; Kennett 1996; Brooks et al. 1997). Furthermore, variation in technique can lead to different counts and growth rings can only be used until a tortoise reaches a certain size. In this study, the maximum number of growth rings that could be distinguished was 33 but it is highly likely that angonoka live much longer than this. Nonetheless, in young angonoka, growth rings were easy to distinguish and may well be deposited annually. Based on growth ring counts and secondary sexual characteristics, angonoka appear to attain sexual maturity at about 15 years of age.

Sample sizes in this study were too small to examine differences among populations; however, it seemed that males from Beheta and West Baly Bay exhibited shell dimorphism at a smaller size, and possibly at a younger age, than in the Cape Sada and West Baly Bay population (Figure 5-8). The mean CL of the 9 adult males at Beheta was 360.2±41.5 mm as compared to > 400 mm CL in the other three populations. This apparent difference warrants further investigation. Variation in size and age at first reproduction is known to occur in populations of aquatic turtles (Cagle 1950; Moll and Legler 1971; Gibbons et al. 1979; Gibbons et al. 1982).

The model developed in this study will eliminate some of the subjectivity in determining sex of adult angonoka. It probably also will allow determination of sex in

subadult tortoises. However, it still will be necessary to use a more invasive method, such as radioimmunoassay technique (Wibbels et al. 1987) or laparoscopy, for determining sex of hatchling and juveniles, unless other distinguishing characteristics can be found (see Graham and Cobb 1998). Given the small size of remaining angonoka populations, it is important to learn as much as possible about the demography of each population. For example, the adult sex ratio of the Cape Sada population is biased toward females (Chapter 2). It would be useful to know the overall sex ratio of the population to determine whether the pattern extends to juveniles. If not, the bias could be a result of differential survival in male and female offspring, or might be a residual effect of past harvest of adult males. If juveniles exhibit a biased sex ratio, environmental factors may be affecting sex determination in the nest.

Table 5-1. Selected measurements of wild angonoka (*Geochelone yniphora*) from the Baly Bay region. CL= straight-line carapace length; CW= carapace width; HT= shell height; PL= plastron length (including gular); GUL= gular; AN= anal notch; AF= anal fork; WBM= wet body mass.

	CL (mm)	CW (mm)	HT (mm)	PL (mm)	GUL (mm)	AN (mm)	AF (mm)	WBM (kg)
Males								
N	35	35	35	35	33	35	35	34
Mean	395.8	269.1	242.2	383.7	77.7	45.3	97.7	9.4
Range	262-481	202-314	166-323	245-478	30.4-110.3	26.1-62.8	47.8-140.8	3.3-15.2
STD	51.4	27.9	29.8	60.8	21.8	9.4	20.1	2.9
Females								
N	37	37	37	36	33	35	35	36
Mean	360.4	257.7	229.8	336.4	58.5	53.6	62.7	8.4
Range	280-405	195-294	173-285	258-406	35.0-98.5	35.0-73.3	47.2-79.0	3.3-12.0
STD	30.5	20.9	22.0	35.3	12.6	8.6	7.4	2.1
Juveniles								
N	56	56	56	54	53	53	53	53
Mean	126.0	95.3	78.2	116.8	15.8	17.4	22.8	0.9
Range	44.0-310.0	38.1-235.0	26.3-200.0	41.8-295.0	3.0-49.2	4.5-49.2	7.0-65.0	0.02-5.9
STD	75.6	54.5	48.9	74.2	13.0	11.9	14.8	1.4
Hatchlings								
N	16	16	16	16	14	16	16	16
Mean	47.2	39.2	27.2	43.2	4.5	7.2	9.2	0.03
Range	43.5-52.0	35.7-41.9	23.8-30.8	38.4-47.0	3.0-5.5	4.6-10.0	6.3-11.0	0.02-0.03
STD	3.0	2.3	2.3	3.1	0.8	1.3	1.3	0.00

Table 5-2. Type III Likelihood Ratio Statistics from logistic regression on morphometric characters of the shell of angonoka (*Geochelone yniphora*).

CHARACTER	DF	ESTIMATE	STD ERROR	CHI SQUARE	PR>CHI
Growth Rings (GR)	1	0.0619	0.0534	1.3816	0.2398
Carapace Length (CL)	1	0.0205	0.0068	11.7175	0.0006
Carapace Width (CW)	1	0.0189	0.0104	3.6048	0.0576
Shell Height (HT)	1	0.0180	0.0101	3.5648	0.0590
Plastron Length (PL)	1	0.0190	0.0057	14.2557	0.0002
Gular length (GUL)	1	0.0596	0.0172	16.6872	0.0001
Anal notch (AN)	1	-0.1134	0.0327	15.6956	0.0001
Anal fork (AF)	1	0.1557	0.0380	57.1713	0.0001

Table 5-3. Type III Likelihood Ratio Statistics from logistic regression using three morphometric characters of the shell of angonoka (*Geochelone yniphora*). Logistic regression was used to build a model for predicting gender in adult angonoka based on the shell characters anal fork (AF), anal notch (AN), and gular length (GUL). The logistic regression equation (π= the probability that the tortoise is a male) is:

$$\pi = \frac{e^{4.2335+(0.1926 \times AF) - (0.9852 \times AN) + (0.4663 \times GUL)}}{1 + e^{4.2335+(0.1926 \times AF) - (0.9852 \times AN) + (0.4663 \times GUL)}}$$

CHARACTER	DF	ESTIMATE	STD ERROR	CHI SQUARE	PR>CHI
Anal fork (AF)	1	0.1926	0.1449	3.2459	0.0716
Anal notch (AN)	1	-0.9853	0.4742	23.9609	0.0001
Gular length (GUL)	1	0.4663	0.2252	10.8369	0.0010
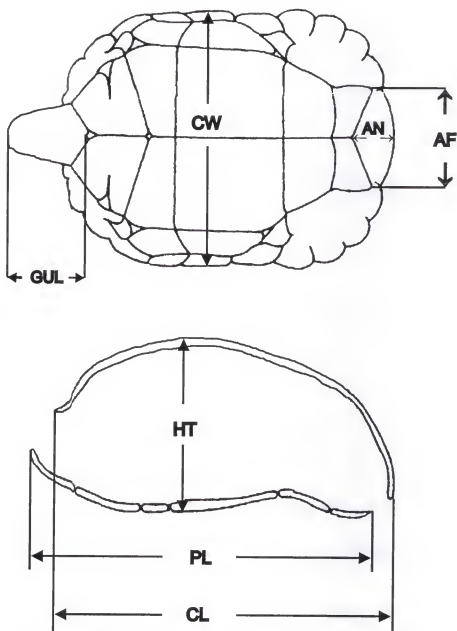
Figure 5-1. Shell measurements taken on angonoka tortoises (*Geochelone yniphora*) in western Madagascar. Measurements included straight-line carapace length (CL), shell height (HT), carapace width (CW), plastron length (PL), gular length (GUL), anal notch (AN), and anal fork (AF). All measurements are in mm.
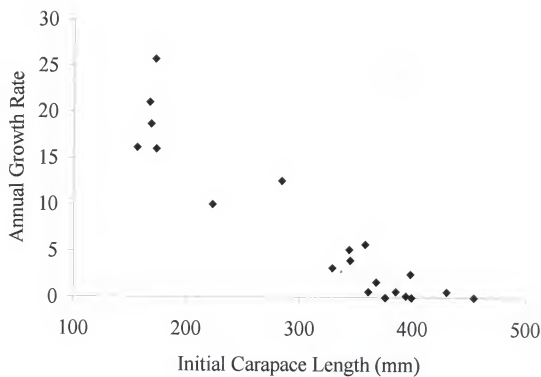
Figure 5-2. Mean annual growth increments for 20 angonoka tortoises (*Geochelone yniphora*) on Cape Sada in western Madagascar.
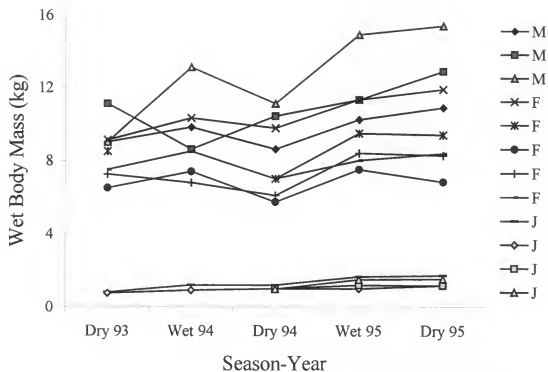
Figure 5-3. Seasonal changes in wet body mass for 12 angonoka tortoises (*Geochelone yniphora*) on Cape Sada in western Madagascar. Measurements were taken from October 1993 through May 1995.

Carapace Length (CL) vs Growth Rings (GR)

Y = -2.26815 + 6.71E-02X
R-Sq = 0.937
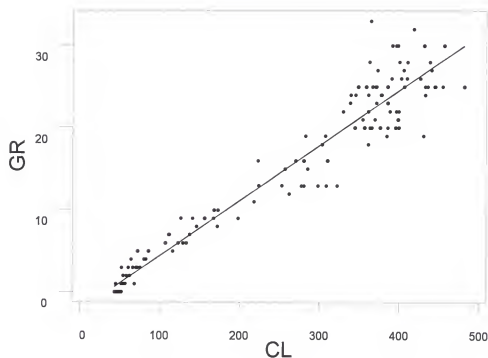
Figure 5-4. Regression line showing the relationship between body size (CL= straight-line carapace length) and shell growth rings (GR) for 143 angonoka tortoises (*Geochelone yniphora*) in western Madagascar.
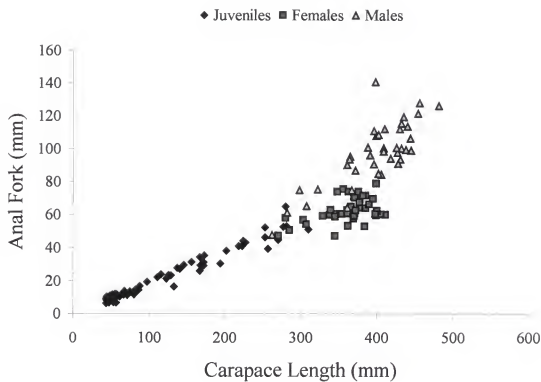
Figure 5-5. Anal fork (AF) measurements as related to body size (CL) in the angonoka tortoise (*Geochelone yniphora*) in western Madagascar.
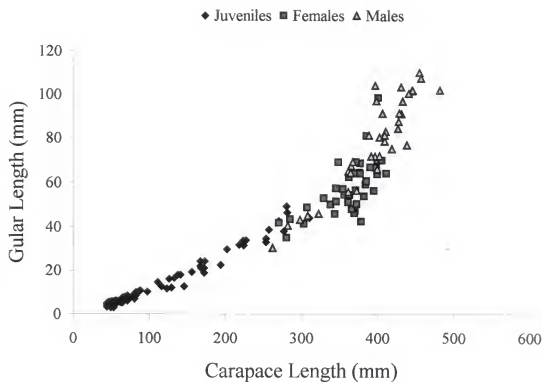
Figure 5-6. Gular length (GUL) measurements as related to body size (CL) in the angonoka tortoise (*Geochelone yniphora*) in western Madagascar.
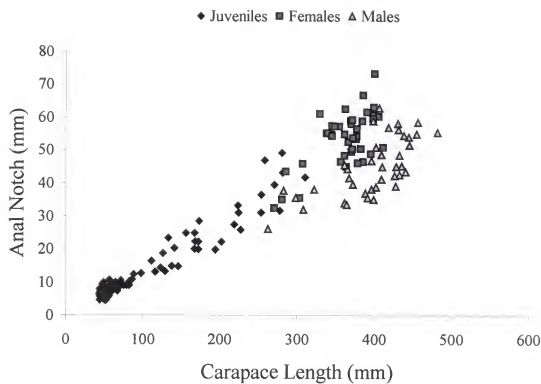
Figure 5-7. Anal notch (AN) measurements as related to body size (CL) in the angonoka tortoise (*Geochelone yniphora*) in western Madagascar.

Figure 5-8. Relationship between carapace length and the number of shell growth rings in adult male angonoka tortoises (*Geochelone yniphora*) from four different populations in western Madagascar.

CHAPTER 6
MANAGEMENT IMPLICATIONS, RECOMMENDATIONS,
AND RESEARCH NEEDS

The angonoka populations identified in this study occur in an area less than 100 km² in size, and this likely represents the entire range of the species. The largest tract of bamboo-scrub habitat occurs west of Baly Bay and is between 4,000-6,000 ha in size. This tract of habitat undoubtedly represents the stronghold of the species. The other four angonoka populations occur on patches of bamboo-scrub ranging in size from <50 to ca. 340 ha. If the remaining habitat supports tortoise densities similar to that of Cape Sada (0.66 tortoise/ha), there may be between 3,100 to 4,400 tortoises in the wild. However, more intensive surveys are needed, particularly in the region west of Baly Bay. The precise extent and quality of bamboo-scrub habitat in this region is not well known. Nonetheless, it appears that angonoka are not as rare as was originally thought (Juvik et al. 1981; Curl et al. 1985).

In the future, population numbers may be limited by the amount of bamboo-scrub habitat available (probably less than 7,000 ha). Tracts of bamboo (*Perrierbambos madagascariensis*) uninhabited by angonoka still exist in the region and should be evaluated as potential sites for relocation or repatriation (but see discussion below). Bamboo seems to be the common component in all remaining habitat patches and these

sites could potentially be restored to bamboo-scrub suitable for angonoka. The importance of bamboo to the angonoka is not known, but results of this study suggest that lesser components of the habitat such as small patches of grass and open rocky areas are important seasonal microhabitats of the angonoka. Grasses and forbs in open rocky areas in the bamboo-scrub habitat appeared to be important food items and grassy areas provided resting sites during the cool, but sunny, dry season. Further research is needed to identify other components of the bamboo-scrub habitat that are important to the angonoka.

Research also should be conducted to determine the impacts of cattle and African bush pigs on the angonoka and its habitat. These species may alter the structure of the habitat (Oliver and Lehr Brisbin 1993) as well as compete with tortoises for food. If bush pigs and cattle are proven to be detrimental to angonoka it may become necessary to exclude them from tortoise habitat. However, fencing would be expensive, difficult to maintain, and likely unpopular with local people (see Curl et al. 1985). Local people should be allowed input into any decision involving use of fences to exclude cattle. Bush pigs are considered pests because they destroy vegetable gardens (Durbin 1993) and could be controlled through periodic hunting or trapping. Local people are reluctant to handle pigs, but it might be possible to hire contract hunters from outside the region to remove pigs.

The role of fire, both natural and manmade, in the Baly Bay region should be investigated. All areas surveyed in this study showed evidence of fire, and the habitat at

Betainalika, Ankasakabe, and Beheta appeared badly degraded. Although paleoecological data indicate that fires occurred in western Madagascar prior to human colonization (Burney 1997), the anthropogenic brush fires that occur today probably have a very different effect than natural fires. Natural fires presumably were ignited by lightning and probably occurred early in the wet season when the vegetation was dry, whereas anthropogenic fires typically are set during the dry season (Durbin 1993). Dry season fires may be more likely to cause direct mortality of angonoka than wet season fires because they are more intense.

Despite frequent brush fires in the Baly Bay region, the aerial extent of deciduous dry forest cover showed little change over an 11-year period (Andrianarivo 1990). Unfortunately, no comparable data are available for bamboo-scrub habitat. Even if the extent of bamboo-scrub habitat has not changed a great deal in the recent past as a result of brush fires, frequent fires may alter the structure habitat. Frequent, unseasonable fires are known to alter the species composition of plant communities (Kruger 1984). Female angonoka on Cape Sada most often nested in scrub-shrub or bamboo, and the loss of these components of the habitat eliminate suitable nest sites. Furthermore, a reduction in vegetative cover may affect incubation temperatures of nests laid in these areas. If angonoka exhibit environmental sex determination, a major change in vegetative cover could influence the sex ratio of offspring. Vegetative cover has been shown to influence the sex ratio of hatchling painted turtles (*Chrysemys picta bellii*) (Janzen 1994) and is

thought to explain a male biased sex ratio in a population of Florida box turtles (*Terrapene carolina baurii*) (Dodd 1997).

Although the effects of fire on the angonoka and its habitat are not fully understood, the remaining habitat should be protected from anthropogenic fires. The creation of firebreaks around angonoka habitat may prevent most fires from spreading from the savanna into the bamboo-scrub habitat. In 1995, villagers helped clear and maintain a firebreak at the eastern edge of Cape Sada. However, a fire was deliberately set on Cape Sada in 1996 (R. Bourou, pers. com.), and in remote areas, it is likely that villagers will continue to burn the bamboo-scrub to drive their cattle from the forest. Local education efforts about the effects of brush fires should continue (Durbin and Ralambo 1994; Durbin et al. 1996).

The establishment of a National Park for the protection of the angonoka is imminent (L. Durrell, pers. com.). Ideally, habitat quality, spatial relationships among the separate populations, dispersal characteristics, and temporal changes in the landscape, all should be considered in designing a protected area (Fahrig and Merriam 1994). However, the design of a reserve for the angonoka is complicated by the fact that the remaining populations are relatively small and isolated from one another. The surrounding landscape contains extensive savanna that is apparently unsuitable habitat for the angonoka. The region also contains a number of small villages, some of which are in very close proximity to tortoise habitat. Local people are accustomed to having access to these areas. Some areas, including Cape Sada have religious significance to local people.

These factors, in addition to biological considerations, should be considered in designing the protected area. It probably will be necessary to allow multiple use of portions of the National Park (e.g., for limited resource extraction or religious purposes).

Although the ideal size of protected areas has been heavily debated, large reserves are undoubtedly better for maintenance of biodiversity and ecological function (Soulé and Simberloff 1986). However, given the extremely limited geographic range of this species and the apparent low population density I think it is critical to protect all angonoka populations, regardless of size. In this case, a reserve is proposed primarily for the protection the angonoka. However, it has been suggested that the reserve include coastal mangrove habitat for the Madagascar fish-eagle (*Haliaeetus vociferoides*). The Madagascar fish-eagle is one of the world's rarest birds of prey and the Baly Bay region is one of only four localities identified for this species (Langrand 1987). The deciduous dry forest west of Baly Bay also should be included in a protected area for the angonoka. Deciduous dry forest has declined greatly in Madagascar (Chauvet 1972; Petter 1987) and this particular tract of forest contains considerable diversity of birds, reptiles and mammals (Hawkins and de Valois 1993). Furthermore, it is possible that the interface between bamboo-scrub habitat and deciduous forest is used by angonoka. If at all possible, the reserve should include all tracts of bamboo-scrub habitat, some or all of the deciduous dry forest west of Baly Bay, and mangroves along the Mozambique Channel in the west.

The spatial distribution of habitat patches should be considered in managing and protecting angonoka populations. The dynamics of fragmented populations have been described as "core satellite", "island mainland" (Boorman and Levitt 1973), "metapopulations" (Levins 1970), or "winking patches" (Wilson 1980) where an asynchronous pattern of extinction and recolonization occurs. Given the current distribution of angonoka populations, if a satellite population becomes extirpated, recolonization is unlikely. I found no evidence that angonoka disperse long distances across savanna, as would be necessary for re-colonization. In fact, a patch of apparently suitable bamboo-scrub habitat less than 1 km east of Cape Sada is uninhabited by angonoka.

Although I did not observe dispersal movements in angonoka in this study, potential routes linking habitat patches should be identified and protected. In other tortoise species young males disperse great distances (Diemer 1992) and the apparent low population densities in the angonoka may be affecting natural migration rates. The West Baly Bay and Betainalika populations could readily be linked as a protected area as no villages lie between these two areas. The populations east of the Bay, Cape Sada, Beheta, and Ankasakabe, probably cannot easily be linked by corridors (see Figure 2-1). These populations should be closely monitored to determine population trends. If populations become depleted to the point where no reproduction is occurring, individuals from other populations could be moved there.

Despite their value in linking genetically isolated populations, corridors can have negative effects by acting as conduits for the transmission of disease and pests (Hobbs and Heunneke 1992; Simberloff et al. 1992). The risk of disease traveling between populations would be particularly high if captive born tortoises were released to the wild (Hess 1994). Even if the released tortoises were disease free, pathogens could travel from free ranging tortoises to naive captive born tortoises.

I feel that reintroduction or augmentation of wild angonoka populations is not warranted at this time. Although rare, more angonoka exist in the wild than was previously thought. Presumably, the current low density of angonoka in the wild is a result of past commercial exploitation and a concurrent reduction in habitat quality due to brush fires. Reproduction is taking place at all populations and if angonoka are no longer collected from the wild, and recruitment into adulthood is occurring, populations could conceivably recover. However, survivorship of juvenile angonoka should be examined. The population structure at Cape Sada is skewed toward adults and small juveniles. This may indicate that juvenile survivorship is low. Only long-term monitoring of individual tortoises can address this question. If juvenile mortality is artificially high, this issue must be addressed before using relocation or repatriation as a conservation tool for the angonoka.

Captive breeding can represent the difference between survival and extinction of a species (e.g., the California condor, the Mauritius kestrel, and the black-footed ferret) (Snyder et al. 1996). In critically endangered species such as the angonoka, captive

populations are invaluable as "warehouses" of genetic material. A great deal of information regarding breeding behavior, reproduction, and feeding also can be collected from captive populations. However, for most species, the value of relocation, repatriation, and translocation (RRT) in conservation is unclear (Griffith et al. 1989; Burke 1991; Dodd and Seigel 1991; Reinert 1991). In a review of 145 reintroduction programs, only 11% reported successful establishment of wild populations (Beck et al. 1994). Furthermore, disease can nullify potential benefits of captive breeding programs and may actually have negative effects on conservation of the species (May 1988; Scott 1988; Jacobson 1993; Cunningham 1996). The causes of a species decline should be addressed prior to initiating RRT programs (Dodd and Seigel 1991; Frazer 1992).

A trial release of captive born juveniles is currently underway at Baly (Pedrono 1997). Five juveniles were released in an area devoid of tortoises, but within several km of a wild population. Prior to release these tortoises underwent a health screening. Preliminary results indicate that captive born juveniles can survive in the wild over the short term (M. Pedrono, pers. com.). However, a number of questions regarding use of reintroduction still remain. It is not known whether angonoka exhibit environmental sex determination. If so, the sex of offspring should be determined prior to their release. If the range contraction and population bottleneck is purely a result of human influence, the remaining "island" populations presumably have been isolated for less than 1,500 years, and are likely not genetically distinct. Nonetheless, the genetic diversity of wild and captive populations should be examined. Genetic relatedness may provide the best

evidence of past connectedness of the extant populations and thus direct future management options. Most importantly, the risk of introduction of disease from captive to wild populations should be weighed against potential benefits of reintroduction. Even with the most rigorous health screening, some pathogens are notoriously difficult to detect. For example, radiated tortoises that were recently returned to Madagascar had been exposed to pathogens not present in wild populations (J. Behler, pers. com.). A pathogen that is thought to have been introduced from captive tortoises into wild desert tortoise (*Gopherus agassizii*) populations in the western U.S. has caused significant mortality in this species (Jacobson 1993).

The discovery of tortoises at Beheta and Ankasakabe that had been previously kept as pets indicates that a protocol should be established for determining the fate of such tortoises in the future. It seems likely that the animals observed in this study were released during the initial phase of the project, before local villagers were aware that it was illegal to keep angonoka as pets. Nonetheless, others may still have tortoises in captivity and attempt to release them in the future. Release of captive tortoises back to the wild should be discouraged unless the specific origin of the tortoise is known and the animal has been captive for only a short period (less than 6-months). This protocol will minimize potential impacts to wild populations including introduction of disease or parasites, or the potential disruption of the social structure of individual populations.

The multifaceted approach to conservation of the angonoka (including education, biological research, and captive breeding) must be continued to insure the survival of this

species. Future research and conservation efforts for the angonoka should focus on protecting and restoring remaining habitat and on monitoring population trends over the long term.

APPENDIX A
HOME RANGE MAPS FOR THREE ADULT MALE,
FIVE ADULT FEMALE, AND FIVE JUVENILE ANGONOKA TORTOISES
(*GEOCHELONE YNIPHORA*) AT CAPE SADA, MADAGASCAR

Adult Male 7

Dry Season
MCP: 4.62 ha
n= 124

100 m

Wet Season
MCP: 45.51 ha
n= 154
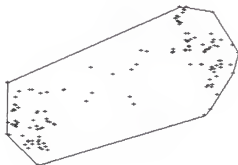
Adult Male 7

Dry Season
KA: 1.38 ha
n= 124

100 m

Wet Season
KA: 28.45 ha
n= 154

Adult Male 13

Dry Season
MCP: 9.12 ha
n= 130

100 m

Wet Season
MCP: 38.32 ha
n= 158
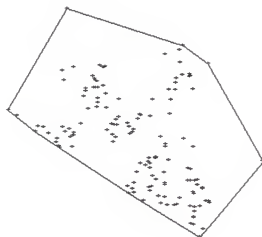
Dry Season
KA: 9.82 ha
n=130

100 m

Wet Season
KA: 16.89 ha
n=158
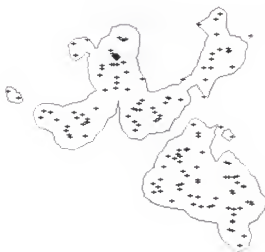
Dry Season
MCP: 13.93 ha
n= 111

100 m

Wet Season
MCP: 31.57 ha
n=118
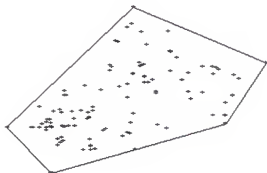
Dry Season
KA: 8.44 ha
n= 111

100 m

Wet Season
KA: 17.91 ha
n= 118

Adult Female 1

Dry Season
MCP: 7.71 ha
n= 140

100 m

Wet Season
MCP: 16.28 ha
n= 163
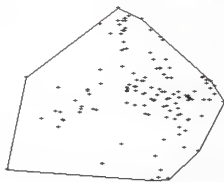
Adult Female 1

Dry Season
KA: 2.97 ha
n= 140

100 m

Wet Season
KA: 10.88 ha
n= 163

Adult Female 3

Dry Season
MCP: 0.95 ha
n= 126

100 m

Wet Season
MCP: 12.47 ha
n= 175
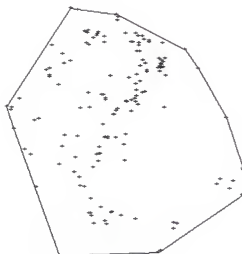
Dry Season
KA: 0.47 ha
n= 126

100 m

Wet Season
KA: 9.06 ha
n= 175

Adult Female 9

Dry Season
MCP: 25.65 ha
n= 123
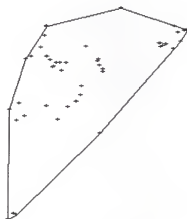
100 m

Wet Season
MCP: 52.07 ha
n=162
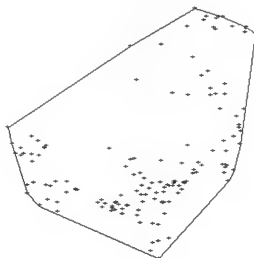
Adult Female 9

Dry Season
KA: 12.53 ha
n= 123

100 m

Wet Season
KA: 28.50 ha
n= 162

Dry Season
MCP: 6.00 ha
n= 127
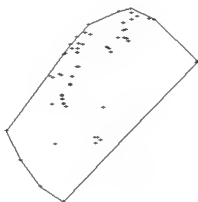
100 m

Wet Season
MCP: 8.04 ha
n= 165
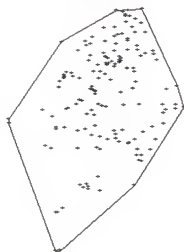
Adult Female 12

Dry Season
KA: 1.26 ha
n= 127

100 m

Wet Season
KA: 4.66 ha
n= 165

Dry Season
MCP: 3.17 ha
n= 110

100 m

Wet Season
MCP: 10.56 ha
n= 154

Adult Female 19

Dry Season
KA: 1.02 ha
n= 110

100 m

Wet Season
KA: 7.63 ha
n= 154

Dry Season
MCP: 0.10 ha
n= 29

50 m

Wet Season
MCP: 1.19 ha
n= 34
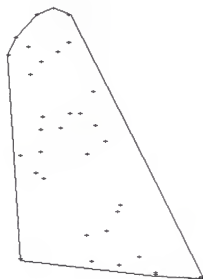
Dry Season
KA: 0.01 ha
n=29

50 m

Wet Season
KA: 0.73 ha
n= 34

Dry Season
MCP: 0.39 ha
n= 108

50 m

Wet Season
MCP: 1.02 ha
n= 148
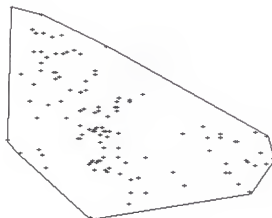
Juvenile 44

Dry Season
KA: 0.22 ha
n= 108

50 m

Wet Season
KA: 0.56 ha
n= 148

Juvenile 51

Dry Season
MCP: 1.77 ha
n= 119
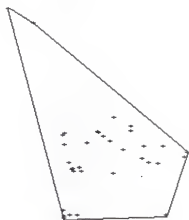
50 m

Wet Season
MCP: 2.19
n= 163
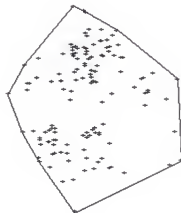
Juvenile 51

Dry Season
KA: 0.78 ha
n= 119

50 m

Wet Season
KA: 1.52 ha
n= 163

Juvenile 83

Dry Season
MCP: 2.19 ha
n= 46
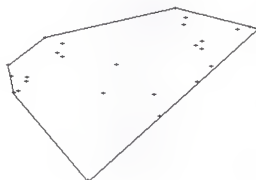
50 m

Wet Season
MCP: 1.87 ha
n= 84
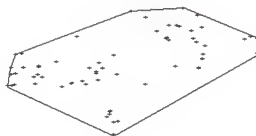
Dry Season
KA: 1.31 ha
n= 46

50 m

Wet Season
KA: 0.99 ha
n= 84

Juvenile 88

Dry Season
MCP: 2.53 ha
n= 38
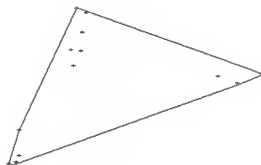
50 m

Wet Season
MCP: 4.83
n= 83
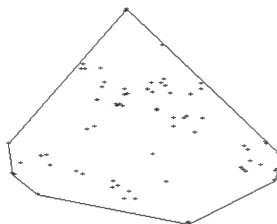
Juvenile 88

Dry Season
KA: 0.57 ha
n= 38

50 m

Wet Season
KA: 4.99 ha
n= 83

APPENDIX B
MORPHOLOGICAL MEASUREMENTS OF
ANGONOKA TORTOISES (*GEOCHELONE YNIPHORA*) IN THE
BALY BAY REGION OF WESTERN MADAGASCAR

IDNO	LOC	SEX	GR	CL	CW	HT	PL	GUL	AN	AF	WBM
C	CS	H	0	43.5	35.9	24.2	38.4	ND	6.1	9.3	0.02
B	CS	H	0	43.6	37.7	26.5	41.3	ND	6.6	6.3	0.02
D	CS	H	0	44.1	36.3	23.8	40.3	4.0	6.4	8.6	0.02
U	CS	H	0	44.3	38.0	28.4	40.1	5.1	4.6	8.5	0.02
R	CS	H	0	44.3	37.1	24.3	39.0	3.3	8.0	8.0	0.02
Q	CS	H	0	44.8	37.7	26.4	40.8	4.4	7.3	9.9	0.02
S	CS	H	0	45.3	35.7	26.0	40.0	3.9	7.3	9.1	0.02
Y	CS	H	0	47.2	39.8	24.7	44.7	4.2	9.4	6.8	0.03
V	CS	H	0	47.6	39.1	28.1	43.3	4.4	7.2	10.3	0.02
P	CS	H	0	48.4	41.2	30.8	44.9	5.5	6.4	10.4	0.03
X	CS	H	0	49.2	41.5	27.3	45.1	3.0	10.0	10.0	0.03
F	CS	H	0	50.1	41.6	30.6	46.6	5.0	7.5	9.5	0.03
H	CS	H	0	50.1	41.1	29.6	47.0	5.1	7.8	10.4	0.03
I	CS	H	0	50.8	41.9	29.2	46.6	5.4	6.5	9.6	0.03
E	CS	H	0	51.0	40.9	27.0	46.9	5.5	8.3	10.4	0.03
Z	CS	H	0	52.0	41.7	28.7	46.4	4.4	5.8	11.0	0.03
K	CS	J	1	45.0	38.1	28.0	41.9	4.6	8.2	9.8	0.02
#10Rt	BET	J	3	51.9	45.1	33.7	47.2	4.2	6.7	9.9	0.04
AA	CS	J	1	52.0	42.2	28.3	46.9	3.9	4.5	8.2	0.03
AB	CS	J	1	52.6	41.8	30.6	47.1	4.9	6.8	8.4	ND
N/A	CS	J	1	53.1	41.9	26.3	45.8	3.0	5.0	7.0	0.04
O	CS	J	1	54.1	44.4	29.5	49.4	5.3	7.6	9.8	0.04
W	CS	J	1	54.1	43.9	30.0	49.1	4.5	7.9	9.1	0.04
AC	CS	J	2	54.4	45.0	31.3	50.1	5.4	7.2	10.5	0.04
M	CS	J	1	54.9	44.4	33.2	50.8	5.9	8.1	11.2	0.04
J	CS	J	1	55.0	45.1	33.8	49.5	5.0	7.4	10.3	0.04

IDNO	LOC	SEX	GR	CL	CW	HT	PL	GUL	AF	AN	WBM
N	CS	J	1	56.6	47.4	35.1	50.5	5.9	8.9	11.9	0.04
T	CS	J	2	58.1	48.9	35.1	54.1	5.4	6.8	10.7	0.04
L	CS	J	3	60.6	48.8	39.4	54.3	5.8	9.2	10.7	0.04
70	CS	J	2	61.7	52.2	38.1	56.5	6.0	9.0	10.4	0.06
G	CS	J	2	62.1	50.8	37.6	56.3	5.4	8.6	10.9	0.05
65	CS	J	4	64.4	52.9	40.2	58.5	5.3	10.1	12.0	0.06
77	CS	J	3	66.5	54.8	41.2	60.1	6.1	9.6	11.7	0.06
A	CS	J	1	68.3	52.9	43.2	60.4	7.3	9.3	12.4	0.08
66	CS	J	3	70.3	56.9	43.8	64.7	7.5	10.1	11.8	0.08
68	CS	J	3	71.3	56.8	47.3	63.9	8.4	10.6	12.0	0.08
67	CS	J	3	71.5	56.5	45.1	62.9	6.1	9.7	11.3	0.08
78	CS	J	3	71.8	57.9	43.1	64.2	7.4	9.4	11.5	0.09
89	CS	J	5	72.5	58.2	45.5	64.5	7.3	9.2	12.1	0.10
69	CS	J	3	75.0	59.2	44.6	68.6	7.4	9.1	13.6	0.10
N/A	CS	J	4	80.5	62.0	49.0	68.7	6.9	9.6	11.6	0.11
74	CS	J	4	82.2	67.5	50.5	73.9	8.4	10.3	14.7	0.11
64	CS	J	5	86.1	67.1	53.9	79.2	10.4	10.9	14.5	0.14
15	CS	J	6	107.0	87.6	71.3	ND	ND	ND	ND	ND
53	CS	J	7	111.0	91.0	79.0	106.0	14.6	16.5	22.1	0.20
1015	WBB	J	7	112.0	86.0	66.0	104.0	ND	ND	ND	0.31
509	BEH	J	5	116.0	93.0	71.0	109.0	12.7	13.1	23.9	0.40
1024	WBB	J	6	123.0	91.0	72.0	113.0	11.7	14.4	21.3	0.38
46	CS	J	9	126.0	98.0	73.0	116.0	16.2	18.7	23.4	0.25
1009	WBB	J	6	129.0	95.3	74.2	119.1	12.2	13.3	23.2	0.40
49	CS	J	6	133.0	104.0	82.0	124.0	16.5	23.4	16.5	0.41
1008	WBB	J	7	137.5	107.1	84.0	130.1	18.1	14.9	27.9	0.43
1004	WBB	J	9	141.0	98.0	73.0	136.0	18.1	20.3	27.3	0.35
63	CS	J	8	146.0	118.0	94.7	138.5	12.7	14.8	29.5	0.40
51	CS	J	9	156.0	118.0	98.0	147.0	19.4	24.9	31.4	0.75
83	CS	J	9	167.0	129.0	104.0	152.0	24.2	24.9	34.3	1.00
1010	WBB	J	9	167.0	123.0	95.0	155.0	22.0	20.0	26.0	0.90
44	CS	J	10	168.0	126.0	103.0	156.0	21.2	22.3	29.3	0.80
88	CS	J	8	172.0	137.0	114.0	161.0	21.2	22.2	31.1	0.85
516	BEH	J	8	172.0	127.0	104.0	161.0	19.0	19.9	29.1	1.10

IDNO	LOC	SEX	GR	CL	CW	HT	PL	GUL	AF	AN	WBM
42	CS	J	10	173.0	131.0	113.0	162.0	24.2	28.5	35.4	1.10
16	CS	J	9	198.0	151.0	125.0	ND	ND	ND	ND	ND
501	CS	J	11	218.0	74.0	132.0	220.0	31.8	27.4	41.1	2.00
1007	WBB	J	13	277.0	214.0	178.0	256.0	38.1	31.7	52.7	4.20
20	CS	J	16	223.0	162.0	146.0	214.0	33.8	33.2	41.1	2.6
91	CS	J	13	224.0	171.0	145.0	209.0	31.5	31.1	44.1	1.9
81	CS	J	13	253.0	186.0	158.0	234.0	34.6	36.5	46.4	3.1
60	CS	J	15	257.0	181.0	157.0	235.0	38.7	47.0	39.5	2.5
86	CS	J	16	270.0	190.0	164.0	258.0	42.6	39.5	44.7	2.8
80	CS	J	16	280.0	235.0	197.0	295.0	49.2	49.2	65.0	5.9
92	CS	J	16	281.0	200.0	171.0	267.0	46.4	43.2	53.1	4.5
82	CS	J	16	310.0	230.0	200.0	292.0	44.1	41.7	51.1	4.2
512	BEH	F	13	280.0	211.0	284.0	267.0	35.0	35.0	58.0	4.5
61	CS	F	15	285.0	195.0	173.0	258.0	43.5	43.5	50.7	3.3
511	BEH	F	18	303.0	221.0	191.0	286.0	41.5	35.5	56.9	5.0
21	CS	F	19	307.0	218.0	196.0	296.0	48.8	45.9	54.4	6.0
3	CS	F	>22	329.0	255.0	203.0	318.0	52.9	61.1	59.1	6.5
55	CS	F	>23	338.0	258.0	285.0	312.0	50.2	55.1	59.8	7.0
87	CS	F	24	339.0	248.0	208.0	272.0	**	55.2	63.0	6.0
9	CS	F	>20	344.0	248.0	220.0	304.0	46.0	54.8	60.4	7.3
8	CS	F	24	345.0	246.0	214.0	322.0	57.4	54.4	58.7	7.0
45	CS	F	>24	345.0	247.0	219.0	319.0	51.5	57.4	47.2	7.6
50	CS	F	>25	348.0	245.0	219.0	349.0	69.2	57.3	73.9	5.5
1003	WBB	F	>26	353.0	248.0	200.0	329.0	65.8	35.5	79.0	7.5
75	CS	F	21	354.0	246.0	214.0	330.0	57.1	57.2	60.4	8.0
519	BET	F	20	356.0	256.0	229.0	344.0	54.5	46.5	75.5	9.0
2	CS	F	25	358.0	269.0	237.0	ND	ND	ND	ND	ND
10	CS	F	>24	361.0	257.0	232.0	333.0	51.2	48.3	60.5	7.5
12	CS	F	>18	361.0	262.0	222.0	299.0	**	54.8	62.7	7.5
71	CS	F	>28	362.0	255.0	228.0	346.0	62.5	62.5	53.4	8.5
517	BEH	F	20	363.0	266.0	240.0	350.0	54.5	45.0	74.0	10.5
1018	WBB	F	>25	366.0	271.0	228.0	339.0	48.1	52.5	64.9	8.9
14	CS	F	>21	369.0	259.0	218.0	333.0	46.3	58.9	57.6	7.5
79	CS	F	>25	370.0	255.0	238.0	359.0	64.1	58.0	59.2	9.5

IDNO	LOC	SEX	GR	CL	CW	HT	PL	GUL	AF	AN	WBM
18	CS	F	>25	371.0	257.0	242.0	349.0	69.3	59.2	70.2	9.2
505	BEH	F	>23	371.0	276.0	237.0	349.0	56.5	50.3	60.7	11.0
1	CS	F	>20	376.0	251.0	226.0	343.0	64.5	53.4	73.9	8.5
1013	WBB	F	>24	377.0	260.0	236.0	353.0	68.7	54.3	64.2	9.6
506	BET	F	>24	378.0	279.0	243.0	359.0	42.5	46.1	69.0	10.5
11	CS	F	>19	384.0	276.0	237.0	353.0	59.2	58.9	53.0	9.5
48	CS	F	>23	385.0	279.0	238.0	306.0	ND	ND	ND	9.1
73	CS	F	>25	385.0	285.0	242.0	388.0	81.1	66.8	64.0	11.2
1020	WBB	F	ND	385.0	278.0	247.0	345.0	60.7	46.5	71.7	11.0
72	CS	F	>26	390.0	264.0	235.0	369.0	67.0	61.6	66.4	9.8
1000	WBB	F	ND	395.0	274.0	245.0	375.0	56.4	48.8	69.7	10.5
62	CS	F	>30	398.0	276.0	249.0	378.0	66.8	59.6	60.3	11.0
19	CS	F	>22	399.0	283.0	242.0	376.0	69.9	63.0	59.6	9.1
6	CS	F	>28	400.0	268.0	236.0	406.0	98.5	73.3	62.3	10.3
43	CS	F	27	405.0	294.0	249.0	396.0	70.0	60.3	60.1	12.0
5	CS	F	16	ND	ND	ND	ND	ND	ND	ND	ND
4	CS	F	ND	ND	ND	ND	ND	ND	ND	ND	ND
1001	WBB	M	12	262.0	202.0	166.0	245.0	30.40	26.10	47.80	3.3
84	CS	M	19	282.0	210.0	183.0	268.0	40.60	37.65	61.15	4.4
500	BEH	M	13	298.0	206.0	192.0	274.0	43.20	35.50	74.80	4.5
515	BEH	M	13	308.0	223.0	195.0	298.0	45.10	32.00	65.20	5.9
503	BEH	M	13	322.0	238.0	202.0	302.0	46.00	38.10	75.15	5.1
85	CS	M	22	361.0	253.0	227.0	354.0	65.15	45.50	64.05	6.0
510	BEH	M	18	361.0	249.0	226.0	339.0	55.80	33.90	90.10	8.0
1011	WBB	M	33	364.0	257.0	260.0	342.0	64.30	33.40	93.60	8.5
502	BEH	M	>20	365.0	248.0	323.0	361.0	67.49	44.30	95.37	7.6
1025	WBB	M	>27	372.0	274.0	237.0	341.0	56.40	39.60	86.80	9.0
514	BEH	M	22	388.0	271.0	235.0	378.0	81.20	36.90	100.90	9.0
507	BEH	M	>30	391.0	255.0	237.0	374.0	71.70	35.50	96.00	9.3
56	CS	M	>30	396.0	267.0	242.0	414.0	104.10	46.80	110.90	7.5
2000	ANK	M	>22	396.0	279.0	246.0	381.0	71.70	38.10	90.60	11.5
13	CS	M	>21	398.0	272.0	224.0	415.0	97.00	58.90	140.80	9.0
513	BEH	M	ND	399.0	267.0	237.0	387.0	66.00	35.00	108.00	10.1
47	CS	M	>26	402.0	265.0	240.0	296.0	80.40	50.80	84.90	8.5

IDNO	LOC	SEX	GR	CL	CW	HT	PL	GUL	AF	AN	WBM
1006	WBB	M	>26	402.0	269.0	237.0	389.0	71.90	38.80	108.50	ND
52	CS	M	>25	406.0	267.0	239.0	407.0	91.30	62.80	84.20	9.5
17	CS	M	>26	409.0	277.0	235.0	398.0	78.50	48.60	100.50	8.0
508	BEH	M	>28	410.0	271.0	280.0	420.0	83.00	45.00	112.00	11.0
1019	WBB	M	32	418.0	293.0	258.0	393.0	75.10	56.90	94.10	11.5
90	CS	M	>26	426.0	284.0	257.0	426.0	84.30	42.20	100.60	10.3
7	CS	M	>19	430.0	282.0	243.0	453.0	103.40	58.10	112.00	11.1
57	CS	M	>30	431.0	275.0	247.0	432.0	91.20	56.20	93.50	9.6
1002	WBB	M	ND	432.0	282.0	252.0	418.0	96.90	48.40	100.30	11.0
2001	ANK	M	>24	432.0	304.0	259.0	389.0	****	42.50	115.40	14.9
1012	WBB	M	ND	435.0	304.0	274.0	354.0	**	45.20	119.40	13.8
58	CS	M	>28	438.0	280.0	247.0	427.0	77.00	54.50	99.50	8.1
1005	WBB	M	>27	440.0	292.0	242.0	444.0	100.40	43.40	113.60	11.0
1014	WBB	M	ND	444.0	284.0	256.0	447.0	101.60	54.00	106.40	11.3
76	CS	M	>25	445.0	295.0	267.0	455.0	101.90	51.45	99.00	15.2
54	CS	M	>25	454.0	299.0	268.0	478.0	110.30	54.90	121.50	9.0
59	CS	M	>30	456.0	310.0	275.0	475.0	107.60	58.50	128.00	11.1
1017	WBB	M	ND	481.0	314.0	268.0	456.0	102.10	55.40	126.30	15.0

Legend: IDNO: identification number. LOC: ANK= Ankasakabe, BEH= Beheta, BET= Betainalika, CS= Cape Sada, WBB= West Baly Bay. Sex: M= adult male, F= adult female, J= juvenile, H= hatchling. GR= shell growth rings. CL= carapace length, CW= carapace width, HT= shell height (mm), PL= plastron length (mm), GUL= gular length (mm), AF= anal fork (mm), AN= anal notch (mm), WBM= wet body mass (kg). ND= no data collected. NA= not applicable. **= no gular. ****= gular removed.

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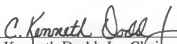
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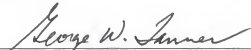
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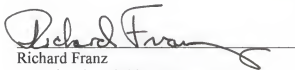
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